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INTRODUCTION

This issue of the International Journal of Comparative Psychology presents six papers given at a symposium on "Comparative Studies of Perception and Cognition" that William C. Stebbins (USA) and I organized for the First European Congress of Psychology (Amsterdam, 1989). These papers illustrate the resurgence of interest in the study of perception and cognition within the framework of evolutionary and developmental processes. Among problems discussed are the estimation of time and the identification and understanding of complex visual and acoustic patterns including social signals. Species as diverse as birds, rats, nonhuman primates and people were investigated. The reports present experimental approaches to methodological issues such as quantification by operant and psychophysical techniques and the delineations of strategies of information processing.

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A CHANGING FOCUS OF ANIMAL PERCEPTION—FROM ABILITIES TO PROCLIVITIES

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ABSTRACT: Several methodologies are available to evaluate how animals discriminate and perceive stimuli. These methodologies are described herein, and the kinds of questions that can be addressed with each technique, and its strengths and limitations, are addressed. Detection and discrimination studies are described that measure animal abilities, followed by classification and judgment studies that measure animal proclivities. The choice of methodology is a consideration in experimental design, because the format of the question can direct, and sometimes define the answer. The experiments discussed emphasize that animals have multiple processing modes available to them that they use to classify stimuli. Detection and discrimination experiments may tap into one of those modes, while categorization and judgment experiments may address a different mode. A feature of these experiments is that they reduce the extent to which we view animal perception and cognition as distinct from human perception and cognition.

Traditional animal psychophysical experiments have been concerned with defining the limits of the sensory systems of animals. For example, they have described the minimum amount of acoustic or light energy detectable as a function of frequency, or the smallest difference in frequency or intensity the animal observer can discriminate (see Stebbins, 1970, and Berkeley & Stebbins, 1990, for pertinent reviews). The focus of these experiments has been on what the animal *can do* when pressed to the limits of its sensory resolving capabilities.

Concurrent with the laboratory studies, ethological experiments have been carried out in the field to assay what animals *do* in their natural environment. These experiments have explored how animals behave in response to the rich variety of stimuli and events present in their native habitat (Beecher & Stoddard, 1990; Nelson & Marler,

1990). The focus of these studies has been to determine how the animal classifies elements of multimodal stimuli.

While both experimental approaches have provided information regarding the sensory, perceptual, and cognitive abilities of many animal species, and while numerous studies using these techniques remain to be done, there have been recent attempts to increase the flexibility of both approaches. Thus, laboratory studies have attempted to explore not only what the animal can do when pressed to the limits of its sensory abilities, but also what the animal does when presented with the option of structuring or classifying stimulus events. Similarly, field efforts have been made to discern how the resolving powers of animals are compromised by the noise inherent in the natural environment. Narins (in press), for example, has made measurements of basic auditory function in the frog, using modified psychophysical techniques, in the natural environment.

This paper discusses animal psychophysical experiments designed to elucidate how animals categorize and organize stimuli (May, Moody, & Stebbins, 1989; Dooling, Brown, Park, & Okanoya, 1990). Detection and discrimination studies, measuring animal *abilities*, are briefly described to give a reference point from which the newer procedures have departed. The limitations of the detection and discrimination methodology, and of field studies, are discussed. We then examine classification and judgment experiments, designed to measure animal *proclivities*. We indicate why these important experiments are particularly difficult to conduct. Finally, we describe the variety of experimental approaches which have been developed to answer classification and judgment questions with animals in the laboratory. Ten to twenty years ago, these approaches were in their infancy. Ten to twenty years from now, we anticipate that new approaches which have emerged from currently used techniques will have enlarged the window through which we can explore the perceptual world of animals.

DETECTION AND DISCRIMINATION EXPERIMENTS IN THE LABORATORY

Most experiments which determine the limits of an animal's sensory capabilities have been similarly designed. Prior to stimulus presentation, the animal performs an observing response, which minimizes activity and optimizes the probability that the animal is attending to the stimulus. In the subsequent presentation of the stimulus, or of a change in the stimulus, the animal performs a reporting response. In positive reinforcement studies, correct detection of the stimulus is followed by food or water, while in avoidance studies, correct detection permits the animal to avoid shock. Premature releases

of the observing response, or false alarms, are discouraged by following these releases with a time-out from the experiment and from the opportunity to receive reinforcement. A feature of the design of these experiments is that the contingencies of reinforcement are clear—all responses made in the presence of the stimulus, or the stimulus difference, are reinforced. There is no ambiguity here—the stimulus is either present or it is not, and those responses made in its presence are reinforced.

Other studies that have helped define the perceptual abilities of animals have used classically-conditioned responses, pairing a sensory stimulus with shock, and presenting these paired stimuli to a water-deprived animal that is drinking. After a number of paired presentations, the animal will stop drinking during the presentation of the sensory stimulus alone, permitting the experimenter to determine thresholds for detection or discrimination. Heffner and Heffner (1985) have used this conditioned suppression procedure to measure absolute auditory thresholds in a wide variety of animal species. An advantage of these operant and classical conditioning procedures is that unequivocal answers are obtained from the animals; a disadvantage is that only a limited subset of questions can be asked, as noted below.

Using the operant conditioning technique, our laboratory has tested the hearing of several species of Old World monkeys, chinchillas (*Chinchilla langier*) and guinea pigs (*Cavia porcellus*). We have determined audiograms representing the minimum amount of energy detectable as a function of frequency for these three species.

We also have used these techniques to explore the minimum detectable difference in frequency and intensity, and the frequency selectivity of monkeys, chinchillas and guinea pigs at a variety of frequencies and sound pressure levels. All of these experiments have refined our understanding of the limits of the auditory system of the species in question. We have determined the effects of the destruction of various parts of the peripheral auditory system on these measures of auditory perception. In Figure 1, we see psychophysical tuning curves, used as a measure of frequency selectivity, from a patas monkey (*Erythrocebus patas*) before and after the selective loss of cochlear outer hair cells. Psychophysical tuning curves are similar in shape to electrophysiological tuning curves, and are thought to be a psychophysical correlate of the electrophysiological measure. They assess the detectability of a probe tone at 10 dB above threshold and a specific frequency, in the presence of pure tone maskers of different frequencies. These functions are plotted as level of the masker needed to mask the probe tone as a function of masker frequency. As seen in Figure 1, in the absence of the outer hair cells, the psychophysical tuning curves are considerably less sharp than in the presence of these cells, suggesting that the outer hair cell system contributes to
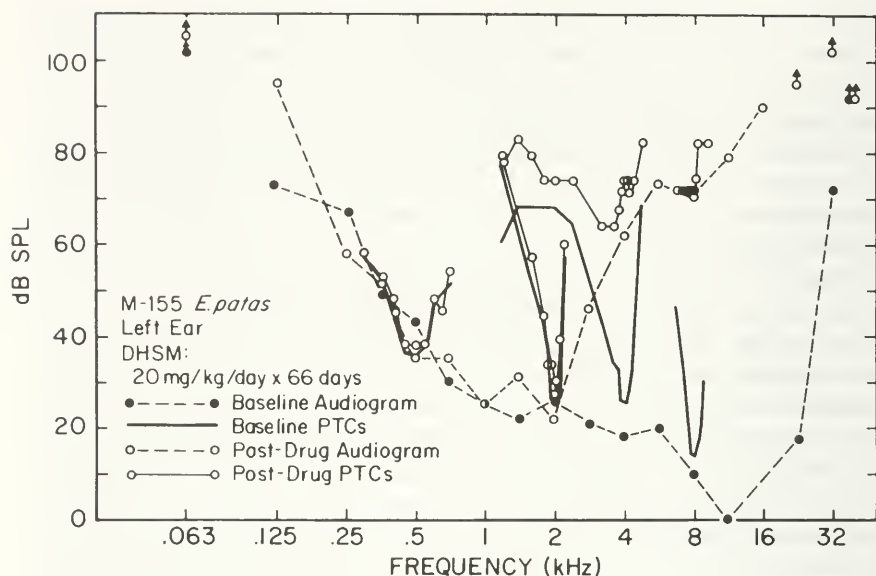
FIGURE 1. A direct comparison of baseline (pre-drug) and post-drug pure-tone threshold curves and psychophysical tuning curves from one patas monkey (*Erythrocebus patas*). These data suggest that the outer hair cell system contributes to frequency tuning in the mammalian cochlea. From "Effects of Outer Hair Cell Loss on the Frequency Selectivity of the Patas Monkey Auditory System," by D.W. Smith, D.B. Moody, W.C. Stebbins, & M.A. Norat, 1987, *Hearing Research, 29*, pp. 125-138. Copyright 1987 by Elsevier Science Publishers BV. Reprinted by permission.

frequency tuning in the mammalian cochlea. Finally, the experimental design employed in these studies can be used prior to conducting experiments which ask how animals classify stimuli, for if they cannot discriminate between the stimuli, they are unlikely to classify them distinctly.

A highlight of these techniques is that they are adaptable to a wide variety of animals, thereby permitting cross-species studies to explore the relationship between structure and function in species whose peripheral sensory systems are distinct. The conditioned suppression technique described above and used by Heffner and Heffner (1985) is a case in point—this methodology has been used to assess absolute auditory thresholds in a wide variety of mammals, including the wood rat (*Neotoma floridana*), least weasel (*Mustela nivalis*), pocket gopher (*Geomys bursarius*), prairie dog (*Cynomys ludovicianus*), cat (*Felis catus*), and guinea pig. A particularly clever adaptation of the operant-conditioning methodology using positive reinforcement was described by Nachtigall (1986), who measured the

chemoreceptive abilities of the dolphin. In these experiments, the dolphins bit a plastic plate, through which distilled water with or without a chemical was dispersed into the mouth. Release of the plastic plate in the presence of a chemical, i.e., a correct detection, was reinforced with a fish. Using this procedure, Nachtigall and his colleagues measured threshold levels for the detection of chemicals which humans describe as sour, bitter, salty, and sweet.

In sum, psychophysical techniques have been used in animals with great success to ask detection and discrimination questions. Issues surrounding reinforcement are clear cut: responses made in the presence of the stimulus are reinforced, while other reporting responses are inappropriate. Researchers differ with respect to how false alarms (reporting responses made in the absence of a stimulus) and misses (failures to respond in the presence of a stimulus) should be regarded when calculating threshold; however, the resultant data from these experiments are relatively unambiguous, and are expressed in terms of the threshold for detection or discrimination. The methods employed in these studies are powerful tools for examining the relationship between structure and function both within and between different sensory systems.

PLAYBACK EXPERIMENTS IN THE FIELD

While determining the limits of an animal's sensory capabilities is relatively straightforward, it is much more difficult to discover how an animal makes use of its sensory capabilities, as noted by Hunt (1986), and it is to this type of experiment that we now turn. The traditional locale for these experiments has been the field. Seyfarth, Cheney, and Marler (1980) designed an exemplary experiment to assess how monkeys respond to acoustically distinct species-specific vocalizations. Free-ranging vervet monkeys (*Cercopithecus aethiops*) give acoustically distinct alarm calls to three different species of predators—leopards, eagles, and pythons. To explore if these calls were functionally distinct to the recipient animals, Seyfarth and colleagues played the alarm calls back to monkeys in the absence of the predators, and watched the monkeys' behavior for 10 s before and 10 s after the presentation of each call. They reported that each alarm call precipitated a distinct set of responses—leopard alarm calls were associated with vervets running into the trees; eagle calls caused the animals to take cover; and python calls were followed by the monkeys looking down. These data suggested that the vervets detected differences in the three varieties of alarm calls (reflecting the monkeys' discriminative abilities), and that they categorized the three types of calls as functionally distinct (reflecting the monkeys' natural organizational strategy).

A second example of asking categorization and judgment questions of animals in their natural environment was carried out by Beecher and Stoddard (1990) in playback experiments using several species of swallows as experimental subjects. Young swallows make "signature calls," presumably to facilitate parent-offspring recognition. Beecher and Stoddard asked if cliff swallows (*Hirundo pyrrhonata*), whose nests are in close proximity to each other, and barn swallows (*Hirundo rustica*), whose nests are more distant, are equally adept at recognizing signature calls emitted by their young. They played the signature calls back to the parents after removing the young from the nest, and measured how often the two species of parents correctly identified calls made by their own offspring. The data suggested that parental recognition of the young by the signature call alone is well-developed in the cliff swallow, but not in the barn swallow.

Based on these field data alone, Beecher and Stoddard might have argued that the auditory discriminative abilities of the cliff swallow were superior to those of the barn swallow. To test this hypothesis, these scientists took members of each species into the laboratory and assessed their ability to discriminate between the signature calls of both cliff and barn swallows. The laboratory data indicated that both cliff and barn swallows could discriminate the calls of the two species, while the cliff swallow calls were more discriminable from each other than the barn swallow calls. Based on the laboratory data alone, one might argue that parent-offspring recognition would occur in both cliff and barn swallows in the field. In sum, neither the laboratory nor the field study alone provided a complete picture of the auditory perceptual capabilities of the two species of swallows.

CLASSIFICATION AND JUDGMENT EXPERIMENTS IN THE LABORATORY

Laboratory explorations of how animals structure and categorize their perceptual world can help bridge this gap. While various experimental approaches have been used to ask classification and judgment questions of animals in the laboratory, all have in common the fact that the *contingencies of reinforcement*, that is, the decision regarding when reinforcement should be delivered, are no longer clear. The potential pitfalls engendered by the uncertainty of when to reinforce were discussed by Herrnstein and van Sommers (1962). In a laboratory study, the experimenter must instruct the animal to respond to the stimulus. But if the instructions are given too narrowly, or the responses are too constrained, the animal's answer becomes trivial. A delicate balance must be struck: the experiment must be designed so that more than one answer is possible, while providing the animal

with adequate instruction regarding what constitutes a correct response. Care must be exercised to not "teach" the animal the correct (i.e., experimenter-predicted) answer to the question. The next sections of this paper describe several experimental approaches which have been used to ask classification and judgment questions of animals in the laboratory. While the experiments that are discussed are by no means exhaustive, the procedures which are described represent the variety of experimental approaches that have been used to date.

Scaling

Scaling experiments, first conducted with humans, are carried out when the stimulus in question varies along one dimension. The intent is to permit the animal to tell the experimenter how it scales a unidimensional stimulus—for example, if the magnitude of the stimulus is increased geometrically, is there a concomitant geometric increase in the perception of the stimulus by the animal? In designing scaling experiments, animals are instructed to respond at different rates in the presence of the training stimuli, and are reinforced for any responses (or, alternatively, *no* responses when testing is carried out in extinction) made to the novel test stimuli. Critics of scaling experiments suggest that during training, the experimenter builds into the animal the very scale she is trying to determine. An early scaling experiment was conducted by Herrnstein and van Sommers (1962) to assess how pigeons scale light intensity. Pigeons were reinforced with food in the presence of a given intensity of light only if they pecked at a response key at an experimenter-chosen peck rate. During these training sessions, Herrnstein and van Sommers used five intensities of light, and five reinforced rates of response. When behavior was well-established, they tested four novel intensities of light, that logarithmically bisected the interval between successive pairs of training stimuli. The data indicated that the pigeons responded to the test stimuli at rates equal to the geometric means of the training stimuli response rates, suggesting that the subjective brightness scale in the pigeon is a power function of light intensity. While this study may have represented a conceptual breakthrough in the design of animal psychophysical experiments, it was subject to the criticism it was designed to avoid. That is, by reinforcing particular rates of response during training, the experimenters may have dictated too closely the answers the animals should give during testing.

Reaction Time Experiments

A second experimental approach used to estimate sensory scales in animals has measured reaction times (RT). These studies are based
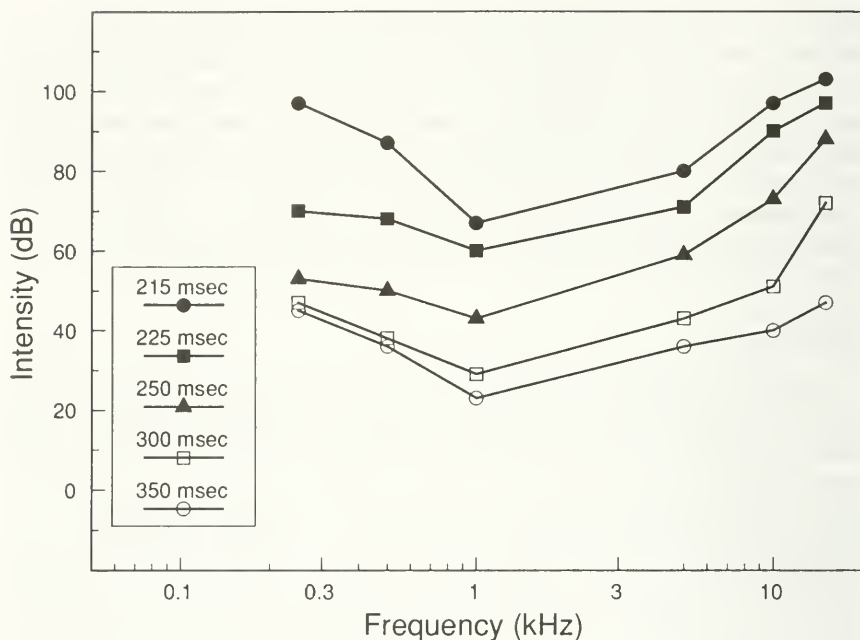
FIGURE 2. Equal loudness contours from one behaviorally-trained crab-eating macaque (*Macaca fascicularis*), where equal loudness was inferred from equal latency contours. Adapted from "Auditory Reaction Time and Derivation of Equal Loudness Contours for the Monkey," by W. C. Stebbins, 1966, *Journal of the Experimental Analysis of Behavior, 9*, pp. 135-142. Copyright 1966 by the Society for the Experimental Analysis of Behavior, Inc. Reprinted by permission.

on the assumption that equal reaction times are measures of equal sensory effect. RT experiments traditionally have been constrained to stimuli which vary in intensity, which severely limited the type of question experimenters could ask of their animals. However, as discussed below, the utility of RT as a tool to explore animal perception has recently increased dramatically by combining it with statistical data analysis techniques, such as multidimensional scaling and cluster analysis (Dooling et al., 1990).

Stebbins (1966) measured equal loudness contours in the monkey using RT as the dependent variable. Figure 2 depicts equal loudness contours for one monkey subject, a crab-eating macaque (*Macaca fascicularis*), where tone intensity is plotted as a function of tone frequency, with each separate function depicting data collected at an equal response latency. Data from humans are similarly configured (Pfingst, Heinz, Kim, & Miller, 1975), reinforcing the hypothesis that equal reaction times in animals measure equal sensory effect.

Generalization Gradient Studies

In generalization gradient experiments, reinforcement is delivered for responses made in the presence of one training stimulus. For example, an animal may be required to make an observing response, and reporting responses are only reinforced when made in the presence of the single training stimulus, such as a pure tone or a photo of a conspecific animal at a particular stage of development. When responding to this one stimulus is well established, generalization testing commences, in which other stimuli along the continuum of interest are presented. Thus, pure tones of different frequencies, or photos of the same animal at different stages of development, are presented. The rate of response to the test stimuli compared to the rate of response to the training stimulus is taken as a measure of the similarity of the stimuli—the greater the difference in response rate, the greater the presumed difference in the stimuli.

The earliest and simplest generalization experiments were conducted in extinction. The purpose of conducting the testing phase of a generalization experiment in extinction is to avoid biasing the animals' responding to the test stimuli. Generalization gradient experiments are not subject to the criticism of scaling experiments—that the experimenter rather than the subject defines the scale to be measured—because only one parameter of the stimulus is reinforced. Further, generalization gradient experiments can assess animal perception along dimensions other than intensity. Mallott and Mallott (1970), for example, trained pigeons to peck at a response disk which had a horizontal line of a fixed length and two vertical end-bars on it. After responding to this training stimulus was well established, they measured response rates to test stimuli. As seen in Figure 3, test stimuli were lines of different length, with either vertical end-bars, like the training stimulus, outward pointing arrowheads on the ends of the lines, or inward pointing arrowheads on the ends of the lines. Using these stimuli, Mallott and Mallott demonstrated that pigeons perceive the Mueller-Lyer illusion in a similar fashion to humans. That is, they found that the pigeons responded at the training stimulus response rate to test stimuli with outward pointing arrowheads only when the length of the test stimulus line was greater than the length of the training stimulus line.

The fact that animals and humans experience illusions similarly suggests that animal perception may share some of the complexities once thought confined to the human perceptual experience. A disadvantage of the generalization technique is that, when the gradients are measured in extinction, their shape changes over time, so that the data must be collected in a single session. Further, the resultant data are often excessively variable.
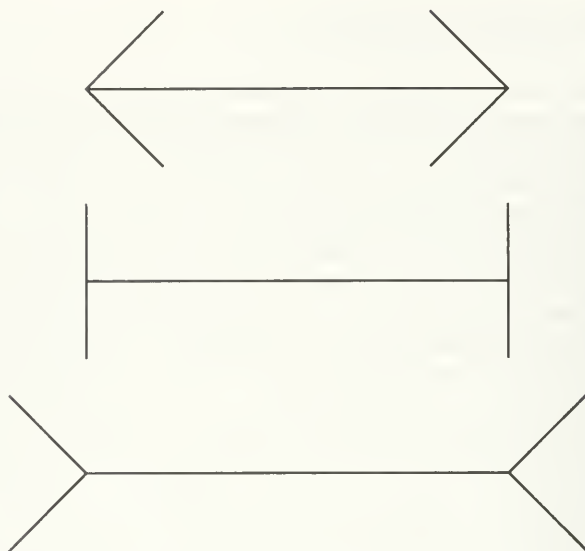
FIGURE 3. Models of the stimuli used by Mallott and Mallott (1970). The middle figure, with a horizontal line and two vertical endbars, represents the training stimulus. All three figures represent test stimuli.

The way in which animals are trained during a generalization study also can influence the shape of the generalization gradient. Jenkins and Harrison (1960, 1962) trained pigeons to peck in the presence of a 1000 Hz tone, and then tested them for their generalization to tones of other frequencies and to silence. They found no generalization gradient; that is, pecking occurred whether the sound was present or not. Does this mean that pigeons cannot discriminate between tones of different frequencies? A second group of pigeons was trained differently; they were reinforced for pecking in the presence of a 1000 Hz tone, but not reinforced for pecking in the presence of silence. When the generalization gradients were assessed in these animals, they were symmetrical against the log of frequency. Finally, a third group of pigeons was reinforced in the presence of a 1000 Hz tone but not in the presence of a 950 Hz tone. The generalization gradients from these animals fell off much more rapidly than either of the first groups. Thus, the structure of the experiment can influence the resultant date, an important point for experimental design considerations which we discuss in more detail below.

Generalization Probe Experiments

An important objection to the generalization gradient procedure, that behavior degenerates when tested in extinction, has been elimi-

nated in recent studies that continue using and reinforcing responses made to training stimuli during testing, while inserting the test stimuli occasionally as unreinforced "probes." As with the other experimental approaches discussed in this section, the intent of these studies is to examine how animals categorize stimuli. During training for a generalization probe experiment, animals are reinforced for responding to stimulus A with response A′ and to stimulus B with response B′. Correct responses are commonly reinforced at a level less than 100% to prepare the subject for the lower level of reinforcement during the testing sessions. This lower level of reinforcement occurs during testing because while the test stimuli are infrequently inserted into the session, responses to these stimuli are neither reinforced nor punished. If reinforcement was maintained at 100% during training, the test stimuli could be clearly identified by the subject during testing, because of the absence of reinforcement following a response to these stimuli. Test stimuli must be inserted infrequently to maintain baseline responding to the training stimuli. The measure of similarity in a probe experiment is how frequently the subject responds to the novel test stimuli as A or as B. Generalization probe experiments result in stable between-subject data, while permitting the experimenter to explore animal perception along many dimensions.

The most severe criticism of this technique is that the experimenter teaches the animal to attend to "unnatural," experimenter-defined categories. Hence, the finding that animals place some novel test stimuli in category A and others in category B may not mean that the experimenter is assessing natural categories formed by the subject, but rather that it reflects that animal's ability to learn to attend to those features of the stimuli which distinguish the categories as defined by the experimenter. Two steps can be taken to mitigate this criticism. First, as discussed below, if species-differences can be demonstrated for category formation, those differences might reflect the fact that the categories are more "natural" for one of the species. Second, if the same categories are formed in experiments that use different methodologies, the confidence in the finding is increased.

The probe technique has been used to explore animal perception in a wide variety of modalities. Herrnstein (1979) used the approach in visual perceptual experiments with pigeons. He trained 4 pigeons to categorize pictures into two groups: those which contained trees, and those which did not. Forty of his training pictures contained trees, and 40 did not. A peck at the response disk in the presence of a tree picture was reinforced with food, while a peck in the absence of a tree picture was not reinforced. After the discrimination was well-established, Herrnstein inserted novel pictures, some containing trees

and some not, and found that the discrimination generalized to the new instances with little or no decrement in performance. This experiment preceded numerous explorations of how the pigeon categorizes its visual world. Researchers demonstrated that pigeons could discriminate fish pictures from nonfish pictures (Herrnstein & DeVilliers, 1980), white oak leaves from other leaves (Cerella, 1979), the letter A from the number 2 (Herrnstein, 1984), and birds from mammals (Cook, Wright, & Kendrick, 1990). Using a similar experimental design, chickens displayed individual visual recognition of a particular chicken (Ryan, 1982). These are categorization and judgment experiments; while the subjects learn to categorize the stimuli, within-category discrimination is quite likely possible.

Generalization probe experiments have been conducted in the auditory modality to explore animal perception of both human and animal communication signals. Kuhl and Miller (1978) examined how chinchillas categorize human speech sounds. Data from humans gathered prior to the Kuhl and Miller study indicated that when presented with a graded continuum of speech sounds, humans often do not attend to the gradation, but rather they classify these speech sounds categorically, a phenomenon referred to as categorical perception. Kuhl and Miller's finding, that chinchillas categorize human speech-like stimuli similar to the way humans categorize them, suggested new ways for speech scientists to conceptualize how speech is processed by the mammalian nervous system. Prior to the Kuhl and Miller study, it was assumed that speech sounds were processed at a "phonetic" level which was restricted to the human nervous system. Kuhl and Miller's data suggested that some human speech sounds may have been selected in the course of evolution because they fall into natural categories which are present in other mammalian nervous systems.

We conducted a similar experiment with Japanese macaques (*Macaca fuscata*), using as training stimuli two calls normally produced by Japanese macaques. Both of these calls were called "coo" calls by Green (1975) who recorded them from monkeys in the field. The two coo calls differed primarily with respect to the temporal position within the call of a transition (peak) from a rising to a falling frequency. The calls were selected because they represented two points along a continuum of relative peak position. The calls also were selected because field research indicated that they were functionally distinct. That is, one of these call types, the "smooth-early-high," is used primarily by young animals out of contact with other troop members, while the other call type, the "smooth-late-high," is used mainly by estrus females as a sexual solicitation. After conducting discrimination training using natural calls as the training stimuli, intermediate stimuli were computer-generated and used as

probes to determine how the Japanese macaques categorized these stimuli (May, Moody, & Stebbins, 1988, 1989). Data from this probe experiment revealed that the Japanese macaques categorically perceived these species-specific stimuli much like humans and chinchillas categorically perceive human speech sounds.

These data suggest that categorical perception may reflect a mode of processing auditory information common to human and nonhuman listeners. Data from control monkey species that participated in the Japanese macaque vocalization study also indicated that there are species-specific mechanisms for categorizing conspecific vocalizations. When speed of acquisition of the discrimination between smooth-early-high and smooth-late-high coo calls was measured, Japanese macaques excelled compared to control species. As noted earlier, this species difference reinforces the hypothesis that the two categories of coo stimuli constitute particularly salient, "natural" categories to the Japanese macaque.

In any scientific study, experimental design might in part dictate the resultant data, as discussed briefly in the generalization gradient section of this paper. This design consideration was demonstrated in the generalization probe experiments with the Japanese macaques (May et al., 1988, 1989). In the experiment, in which responses to the intermediate test stimuli were neither reinforced nor punished, the data suggested that the smooth-early-high and the smooth-late-high stimuli were categorically perceived as a member of one group or the other, as seen in Figure 4. But in a second experiment, May and colleagues asked if animals could discriminate between these stimuli. In one variant of this procedure, one of the stimuli (the standard) was repeatedly presented; when this stimulus changed to one of the other stimuli along the continuum (the comparison stimulus) and the monkey released the response cylinder, he was reinforced. Now, the animals demonstrated that they could discriminate between all of the stimuli located along the continuum, with only slightly better discrimination behavior at the category boundary, as seen in Figure 4.

These categorical perception data may seem contradictory—is categorical perception an epiphenomenon, or is it a universal mode of perceiving communication signals even from other species? But within this apparent contradiction lies an important distinction in perception—that animals, and humans, have multiple processing modes that they use to classify stimuli. Many people say "hello" when greeted, and human listeners regard all the variations of these acoustically distinct stimuli as having the same meaning. However, these same stimuli are easily discriminated. Similarly, the Japanese macaque data suggest that the psychophysical method used to study acoustic communication in the monkey may strongly influence the processing mode applied to the stimuli. The discrimination procedure
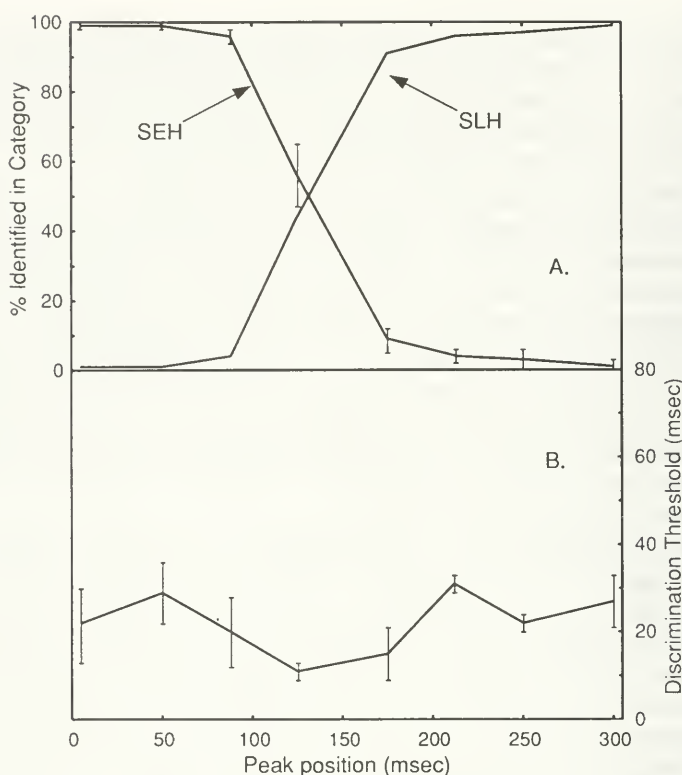
FIGURE 4. A. Identification of synthetic contact "coo" calls by Japanese macaques (*Macaca fuscata*). SEH designates smooth-early-high calls, in which the temporal position of the peak frequency of the call occurred early, while SLH designates smooth-late-high calls, in which the temporal position of the peak frequency of the call occurred late. Data are presented as mean and standard error of the mean for four Japanese macaques. A category boundary, as indicated by the sharp transition in the behavioral response, was observed near the midpoint of the peak position continuum. B. Discrimination thresholds, in ms, for the synthetic vocal stimuli. Data are presented as mean and standard error of the mean for the four Japanese macaques. Data are replotted from "Categorical Perception of Conspecific Communication Sounds by Japanese Macaques, *Macaca fuscata*," by B. May, D.B. Moody, & W.C. Stebbins, 1989, *Journal of the Acoustical Society of America, 85*, pp. 837-847. Copyright 1989 by the Acoustical Society of America. Reprinted by permission.

directed the monkey's attention to small changes in the acoustic dimension of the stimuli, while the probe procedure encouraged phonetic processing while discouraging attention to minor acoustic variations in the stimuli which lacked communicative relevance. The hypothesis that multiple modes are available to animals to process complex stimuli is discussed below.

Multidimensional Scaling

Another technique available to animal psychophysicists which recently has gained increasing acceptance asks animals to perform a simple discrimination task. The data, however, are analyzed with statistical techniques, such as cluster analysis and multidimensional scaling. While these experiments are time-consuming, they permit the experimenter to draw conclusions about how the animals organize stimuli. This procedure has been used to determine how monkeys categorize pictorial stimuli (Hunt, 1986), how pigeons segment visual stimuli which differ along multiple dimensions (Blough & Blough, 1990), and how budgerigars process both simple and complex, species-specific vocalizations (Dooling et al., 1990). These experiments have enriched our understanding of the perceptual proclivities of animals by asking categorization and judgment questions—questions that are difficult to frame using some of the methodologies described above because the format of the question defines the answer. In experiments using these procedures, animals perform an observing response in the presence of a single stimulus, and a reporting response any time the stimulus changes. Either the speed of reporting "stimulus change" (the reaction time), or the frequency of this report (the percentage of correct detections for each stimuli pair), then can be entered into a similarity matrix. Shorter reaction times or a higher percent correct to pairs of stimuli in these experiments indicate that those stimuli are less similar than other pairs of stimuli which take longer to discriminate or are less frequently identified as different. The statistical procedures can be used to evaluate *how* similar the stimuli are by plotting the data in a three-dimensional format presumed to reflect how the animals categorize the stimuli. An advantage of this technique is that the decision regarding when to reinforce a response, the *contingencies of reinforcement* problem addressed earlier, is straightforward—any response made to a pair of stimuli that differ is reinforced. While the methodology encourages the animals to discriminate between stimuli, thereby clarifying the contingencies of reinforcement, the statistical data analysis permits the experimenter to assess categorization. Multidimensional scaling procedures are described in more detail by Dooling et al. (1990); they represent a pow-

erful new technique for conducting future categorization and judgment experiments in the laboratory.

Unconditioned Responses

A final technique available to the experimenter investigating animal perception makes use of unconditioned, "natural" responses. Caution is encouraged in designing and interpreting these experiments, because of the possibility of experimenter bias in determining when a response occurred, and the fact that responses may habituate with time. With this in mind, several carefully controlled studies using unconditioned responses as the dependent variable have enjoyed considerable success in investigating animal perception. Humphrey (1974) and Perrett and Mistlin (1990) explored how monkeys perceive visually presented information. Humphrey examined the amount of time monkeys looked at pictures, and noted that after seeing one picture of a cow, the monkey spent much less time looking at a second picture of a cow, whereas after looking at one picture of a conspecific monkey, other pictures of conspecific monkeys were proportionately more interesting. Perrett and Mistlin reported that stump-tailed macaques (*Macaca arctoides*) gave an appeasement response (teeth chattering and lip smacking) more frequently to pictures of monkey faces making eye contact than to pictures of monkey faces with the eyes averted. These scientists argued that if such untrained responses are provoked consistently more to one type of stimulus than to a second, the ability of the animal to perceive the difference between the stimuli may be inferred.

CONCLUSION

Recent advances in the design of animal psychophysical experiments permit scientists to explore the perceptual world of animals in greater detail—not only to determine the limits of the animals' sensory systems, but also to examine how animals use incoming perceptual information. While these studies have augmented information already available about animal sensation, they also have fundamentally changed the way we regard animal perception. Herrnstein (1984) suggests that the ability to categorize stimuli confers such an evolutionary advantage that it may be universal among all living organisms. Nelson and Marler (1990) discuss in detail the advantages and disadvantages of categorization, when an animal "lumps" stimuli together, versus when it "splits" stimuli into distinct categories. Too much lumping, while rapidly reducing complex information into a small number of categories, may neglect variation critical for an ani-

mal's survival. Alternatively, too much splitting renders every experience unique. The distinction we have drawn in this paper, between what animals are capable of, and what they do, is similar to Nelson and Marler's (1990) differentiation of the "just-noticeable-difference" (JND) and the "just-meaningful-difference" (JMD). While the JND has an established definition in both human and animal psychophysics, the JMD is a new term, reflecting the minimal difference between natural stimuli which elicits a measurable difference in the nature or the intensity of a natural response to a particular signal class. Beecher and Stoddard (1990) address the same distinction with yet a different terminology: "discriminable," but "biologically-equivalent" stimuli.

Earlier in this paper, we suggested that organisms have available to them multiple modes of processing complex stimuli. Detection and discrimination experiments may tap into one of those modes, while categorization and judgment experiments may address a different mode. Hulse, Page and Braaten (1990) have suggested that these modes may be arranged hierarchically, such that while one mode is possible, it may function normally as a secondary strategy, with an alternative strategy being the primary processing mode. Earlier, Marler (1982) suggested that there is a species-specific hierarchy of attentional preferences for perceptual cues. The experiments described in this paper are designed to examine these different perceptual strategies; the design of the experiment can dictate which processing mode is selected by the animal. One feature of these experiments is that they reduce the extent to which we view animal perception and cognition as distinct from human perception and cognition. The histories of philosophy and psychology are filled with attempts at distinguishing humans from animals along a variety of dimensions. Once it was assumed that while humans categorize, animals discriminate. Recent laboratory experiments suggest that the difference is in degree rather than in kind.

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SOCIAL SIGNALS ANALYZED AT THE SINGLE CELL LEVEL: SOMEONE IS LOOKING AT ME, SOMETHING TOUCHED ME, SOMETHING MOVED!

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ABSTRACT: In the superior temporal sulcus (STS) of the macaque brain there are populations of cells which respond selectively to faces. Studies of these cells reveal that they are very sensitive to the direction of eye gaze and posture of the head of other subjects. It is argued that one function of the cells is to enable analysis of where other individuals are directing their attention. Given this selectivity for complex socially relevant stimuli it is surprising that the STS contains cells that respond to touch anywhere on the body or to any movement seen in the visual environment. We have investigated these tactile and motion sensitive cells to determine their behavioural significance. In the awake, behaving monkey we found that the critical dimension for polymodal coding is whether or not the sensations are expected. Tactile stimulation out of sight cannot be predicted and elicits neuronal responses. By contrast, when the monkey can see and, therefore, predict impending contact, or when the monkey touches a familiar surface in a predictable location, cell responses are reduced or abolished. In an analogous way some cells are unresponsive to the sight of the monkey's own limbs moving but respond to the sight of other moving stimuli. Since unpredictable sensations are often caused by other animals, the STS area appears well suited to defining sensory stimuli that are important in social or predator/prey interactions.

INTRODUCTION

We have been studying the properties of single neurons in one region of the association cortex of the macaque monkey. Figure 1A illustrates a side view of the brain with the site of study indicated with cross hatching. Visual information arrives in the cortex at the back of the brain and has been processed in several prestriate regions before reaching the study site within the superior temporal sulcus (STS) (Jones & Powell, 1970; Seltzer & Pandya, 1978). The STS also receives anatomical input from the parietal association cortex, an

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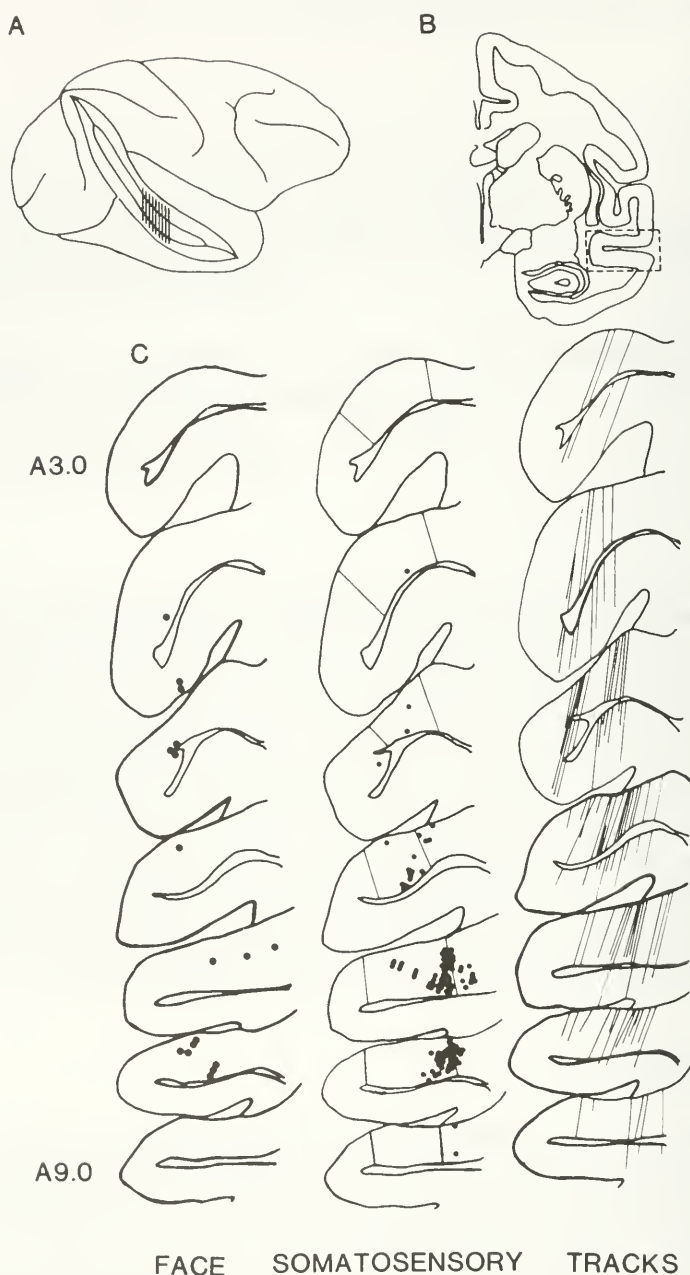
FIGURE 1. Histological location of study site. (A) A schematic drawing of a sagittal view of a rhesus macaque brain showing the position of recordings (cross-hatching) within the opened superior temporal sulcus (STS). (B) A coronal section of the right hemisphere with a box around the STS. (C) Serial coronal sections illustrating the distribution of cells selectively responsive to faces (left) and somatosensory stimulation (middle) and the location of electrode trajectories (right).

area involved in processing tactile and visual information and in motor control (Hyvärinen & Poranen, 1974; Mountcastle, Lynch, Georgopoulos, Sakata, & Acuna, 1975; Lynch, Mountcastle, Talbot, & Yin, 1977; Leinonen, Hyvärinen, Nyman, & Linnankoski, 1979; Seltzer & Pandya, 1984). The STS projects to a variety of brain systems but has particularly strong connections with the amygdala, a system implicated in the control of social and emotional behaviour (Aggleton, Burton, & Passingham, 1980).

The STS is involved in processing a variety of information in visual, auditory, and somatosensory modalities (Bruce, Desimone, & Gross, 1981). For the visual modality a number of studies have reported cells selectively responsive to complex stimuli such as hands and faces (Gross, Rocha-Miranda, & Bender, 1972; Perrett, Rolls, & Caan, 1982; Rolls, 1984; Baylis, Rolls, & Leonard, 1985). Given the selectivity of cells for faces and the connections with the amygdala, it is argued that the STS might function to provide an analysis of stimuli relevant to social interactions.

In the first half of the paper it will be argued that one of the main functions of the analysis is to provide cues to where other individuals are directing their attention. This functional role has been largely overlooked in studies describing sensitivity to different perspective views of the head (Bruce et al., 1981; Desimone, Albright, Gross, & Bruce, 1984; Perrett et al., 1982; 1985a; Perrett, Mistlin, & Chitty, 1987; Perrett, Mistlin, & Harries, 1989a; Perrett, Harries, Mistlin, & Chitty, 1989b; Perrett et al., 1989c; Hasselmo, Rolls, Baylis, & Nalwa, 1989).

The function of sensory information processing in other modalities in the STS has been less obvious since much of the processing seems to lack selectivity (Bruce et al., 1981; Hikosaka, Iwai, Saito, & Tanaka, 1989). Consideration of the difference between sensations arising from the monkey's own movements and social interactions involving the actions of other individuals, however, reveals that STS processing of somatosensory information is also highly selective (Chitty, Mistlin, & Perrett, 1985; Mistlin, Perrett, & Chitty, 1986; Mistlin & Perrett, 1990; Perrett, Mistlin, Harries, & Chitty, 1989d).

The second part of the paper is devoted to a consideration of the processing of somatosensory information and visual motion in the STS. Cells in the STS appear to be selectively responsive to sensory events arising from other individuals and are able to ignore the equivalent but predictable sensations that are self-produced.

The capacity to ignore predictable self-produced sensory input has received little consideration except for research on the stabilization of the visual world independent of eye movements (Wallace, 1985; Galletti, Battaglini, & Aicardi, 1988). Despite this, the discrimination between self-produced and nonself-produced events is proba-

bly fundamental to information analysis in sensory systems through-out the animal world (Sperry, 1950; von Holst & Mittelstaedt, 1950; Bell, 1989). The sensitivity of STS cells to unexpected stimulation allows them to be preferentially activated by stimuli arising from other individuals. This capacity could allow them to play an impor-tant role in detecting predators and in social interactions with other monkeys.

I. SENSITIVITY TO HEAD POSTURE AND TO GAZE DIRECTION

Recordings from the STS have revealed populations of cells that respond selectively to faces and other views of the head (Perrett et al., 1982, 1985a). The first part of the paper reviews studies of cells re-sponsive to the head that we have made over the last 10 years. We describe a theoretical re-evaluation of cell function and recent devel-opments in our analysis of how information relevant to social interac-tion (posture and gaze) affects discharges in these cells. Head posture and direction of gaze are signals which play an important role not only in human society (Argyle & Cook, 1975) but also in nonhuman primate societies (Perrett & Mistlin, 1990). For example lowering of the head and direct eye contact for monkeys are components of threat gestures (Bertrand, 1969; Hinde & Rowell, 1962; van Hoof, 1967). The act of averting the head and gaze may act as a submissive signal (Chance, 1962; Redican, 1975; Perrett & Mistlin, 1990).

GENERAL METHODS

We recorded the activity of single cells in awake behaving mon-keys (5 *Macaca mulatta* and 2 *Macaca arctoides*). From 500 to 1,500 cells were studied in the temporal cortex of left and right cerebral hemispheres of each monkey. Details of recording techniques are given in brief here (for details see, Perrett et al., 1985a, 1985b). Be-fore recording work began, the experimental animals were trained to sit in a primate chair and to perform visual discrimination tasks, giv-ing a lick response for a fruit juice reward. This ensured that they attended to visual stimuli presented. When trained, a 15 mm stain-less steel ring (recording chamber) was attached to the skull under barbiturate anaesthesia and full sterile surgical procedures. One month later, recordings began and were made 2-3 times a week for approximately 1 year. During each recording session (1-4 hours) the animal was seated in the primate chair. A miniature hydraulic micro-drive was attached to the stainless steel recording chamber and a small microelectrode (insulated tungsten wire with an uninsulated

tip 10 microns diameter, 10-15 microns long) was advanced into the cortex of the temporal lobe. Between recording sessions the microelectrode was removed and the monkey was returned to its home cage.

The electrical activity from the brain recorded through the microelectrode was amplified and signals outside the relevant band (0.5-20 kHz) filtered. Brain activity was visually displayed on oscilloscopes and action potentials from an individual cell selected on the basis of voltage amplitude and duration. These were arranged to trigger digital pulses which were then analysed by computer. Real or photographic visual stimuli were presented from behind an electromagnetic shutter (Compur, 6.4 cm aperture). Each cell was tested with a range of different views of the head and body, and a range of different directions of motion. Where cells were found responsive a variety of other control stimuli were studied. The responses of individual neurons to 3-D or 2-D stimuli were measured during the period 100-350 ms after the presentation of a stimulus. This period was chosen because the majority of cells in the temporal cortex responded with latencies of 100-150 ms. The position of cells recorded in each hemisphere was reconstructed from histology and frontal and lateral xrays taken at the end of each recording track (e.g., Figure 1).

RESULTS

Different populations of cells in the temporal cortex responded to different types of stimuli. For different experimental subjects, 40 to 60% of cells remained unresponsive during testing and were unclassified. Of the classified cells, on average 46% responded to static visual stimuli; 10% selectively to the sight of the head or body; 4% to objects other than bodies and 32% without apparent form selectivity. Thirty-eight percent of the classified cells were motion sensitive; 11% responding selectively to body motion; 2% responding to objects other than bodies moving and 25% responded to particular types of motion without form selectivity (Perrett et al., 1985b, 1989d; Perrett, Harries, Benson, Chitty, & Mistlin, 1990a; Perrett, Harries, Chitty, & Mistlin, 1990b). Sixteen percent of the classified cells responded to tactile or auditory but not visual stimuli.

This section deals only with those responsive to different views of the head. The proportion of cells in the upper bank of the STS that were found selectively responsive to the face and head varied from study to study, ranging from 1-20% (average 10%). This variation probably reflects a modular or clumped organization of cortex, and possible asymmetry in hemispheric distribution (Perrett et al., 1988). Within a clump extending 3-4.0 mm across the temporal cortex cells

have a higher probability of responding to the same type of stimulation than outside the clump (Perrett et al., 1984, 1985a, 1985b, 1987).

In an early study of 182 cells selectively responsive to the sight of the head, 63% were found to be sensitive to perspective view of the head (Perrett et al., 1985a). Discrete populations of cells were found to be maximally activated by different views of the head. In the horizontal plane separate populations were found to be selective for the face, left and right profile, and back of the head views. In the vertical plane, two further types of cell were found to be selective for head raised and head lowered.

THE USE OF CHARACTERISTIC VIEWS FOR RECOGNITION

For several years we assumed that the function of the cells responsive to faces and to other views of the head was to facilitate the recognition of the stimulus as a head (Perrett et al., 1984, 1985a, 1987) or as an individual, since some cells were sensitive to the differences between faces (Perrett et al., 1984, 1989a, 1989b, 1989c; Baylis et al., 1985). We argued that cells were tuned to particular perspective views because the views were visually different. If recognition was to be successful from all views then different views would need to be separately coded. Cells tuned to the face and other views of the head show considerable generalization for the preferred view despite changes in retinal position (Desimone et al., 1984; Bruce et al., 1981; Perrett et al., 1989a), size (Perrett et al., 1982, 1984; Rolls & Baylis, 1987), orientation (Perrett et al., 1984, 1985a) and lighting (Perrett et al., 1984). Cells tuned to one perspective view can therefore be seen as providing a high level description covering almost all instances of that view.

It can be argued that only a limited number of such high level discriptions need to be constructed to cover all the possible ways in which a head can be seen. From the initial studies of view (Perrett et al., 1985a) it appeared that cells were selectively tuned for just four "characteristic" views in the horizontal plane (face, left and right profiles and the back of the head). Although cells were sensitive to change in perspective view tuning for view was fairly broad. For most cells, rotation of the head 60 degrees away from the optimal view reduced the rate of response to only half that of the optimal view (Perrett et al., 1985a; Perrett et al., in press). Thus, populations of cells tuned to the four characteristic views could cover intermediate views such as the half profile. The notion of selective coding of particular characteristic views accords with the results of some psychological experiments and current ideas in mathematical and computational approaches to visual recognition (see Perrett & Harries, 1988, for review).
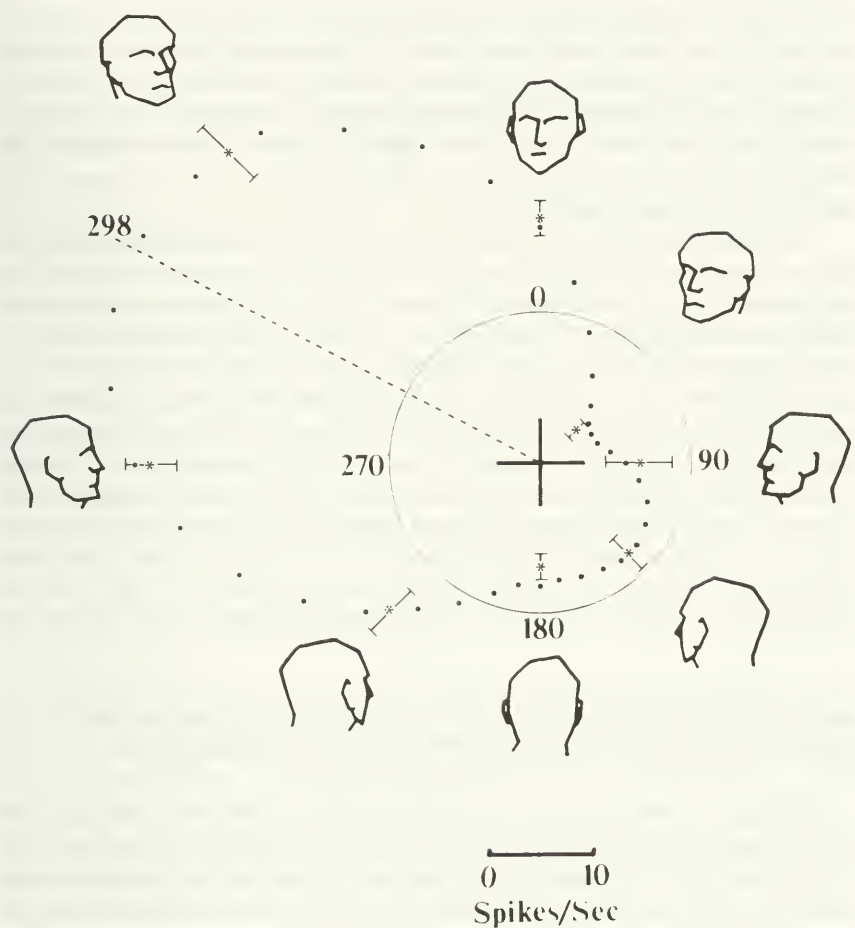
FIGURE 2. Sensitivity to perspective view of the head in the horizontal plane. The magnitude of one cell's response (mean $+/-$ 1 S.E. from 10 trials) to 8 different views of the head is illustrated by the distance from the central cross to the star (bracketed by the error bars). A schematic illustration of the head view at different angles is given around the perimeter. The dotted line provides an interpolation of the cell's tuning curve to different views, it plots the best fit second order cardioid function relating observed response to angle of view. The estimated angle of view producing maximal response is indicated by the dashed line. The central solid circle denotes the level of the cell's spontaneous activity.

Having coded each of the separate views, outputs could be pooled to establish a description of a head or person which holds from all views. This level of coding is comparable to the object centred coding of Marr and Nishihara (1979; Marr, 1982). It should be noted, however, that their model constructs object centred representations directly from surface orientation and does not use an intermediate stage representing specific views.

Results from recent physiological studies confirm the selectivity for perspective view but indicate that cells are tuned to *many* different views. The optimal views for individual cells are not restricted to the four prototypical views (Perrett et al., 1989a; Hasselmo et al., 1989; Perrett et al., in press). Figure 2 illustrates the tuning of one cell to different views of the head in the horizontal plane. This cell is maximally responsive to the half profile view of the head (rotated to the monkey's right by approximately 45°). The preferred view is, thus, directly in between the proposed face and profile characteristic views. From the arguments above it seems then, that more views are coded than are needed to allow recognition from any view. This then presents a puzzle as to *why* so many views are coded. If they are not necessary for object recognition what are they for?

CELLS TUNED FOR DIFFERENT VIEWS OF THE HEAD: A ROLE IN RECOGNIZING FACES OR DIRECTION OF ATTENTION

The cells responsive to the sight of the head may not have one single function. By exploring other possible functions it may be possible to provide an account of why so many views receive separate coding. One account makes the assumption that a cell's function is to detect those stimulus dimensions to which it is maximally sensitive. When a head is observed, the variation in response across the view sensitive cells in the STS could provide collectively an accurate description of the direction in which the head is pointing relative to the observer. Perhaps this then is a function of the cells; to specify the head direction. Such coding could provide an index of where other individuals are directing their attention. A cell maximally responsive to the left profile thus provides a signal that the attention (of another individual) is being directed to the observer's left. Such information is undoubtedly useful for analyzing a great variety of social interactions between other individuals, working out who is threatening whom, who is soliciting support from whom, and whether one's infants or "friends" are being approached, threatened, etc.

One could ask again why so many views need to be coded to specify direction of another's attention. Here the question is misdirected; if one is attempting to recognize a person, then head orientation

(view) is an irrelevance to be overcome, but if one is coding direction of an individual's attention, then the head orientation is useful. The more accurately the STS cells can specify head view, the more accurate the inference about the direction of attention. Thus while recognition needs only a few key views to be selectively coded, the analysis of where someone else is facing (and directing attention) benefits from having a wide range of head views selectively activating different cell populations.

If only four head views (face, left and right profile and back of head) were coded, then recognition of the half profile and other intermediate views would require a comparison between the amount of activation of the populations tuned to the four views. A left half profile would be indicated if face and left profile views were activated to an equal extent and the other two characteristic views were not activated. With a whole range of views explicitly coded (activating different cell types) then further processing is less complicated. View or direction is indicated by the maximally activated cell type.

VERTICAL HEAD ORIENTATION

The ascription of this social function to cells coding head view also makes sense of the tuning observed in many cells to head posture in the vertical plane (Perrett et al., 1985a). Two classes of cells were found to be selective for the head down and the head up. These cells generalized across change of perspective view in the horizontal plane. Cells coding the raised head responded to the face, profile and back of the head views when the head was raised. Similarly cells coding head down generalized across front, side and back views of the head when the head was lowered.

It is difficult to see why generalization should exist only for head up views and not extend to head level views if the cells have a function in recognizing the object as a head from any view. By contrast an account based on directed attention naturally extends to cover the generalization. All views of another individual with head raised indicate a focus of attention directed somewhere above the viewer's head. Similarly all views of the head down imply a focus of attention low in the environment, below the observer.

GAZE DIRECTION

In most cases the direction in which an individual's head is pointing is a good index of where his or her attention lies, but gaze direction is a better guide to focus of attention. This leads to several pre-

FIGURE 3. Sensitivity to head and eyes directed to the viewer in the horizontal plane. Upper: schematic representation of stimuli used for testing. Lower: mean and standard error of the responses of one cell (M047) to the stimuli. S.A. = spontaneous activity. [Number of trials per condition (N) = 6, 5, 4, 4, 3, 4, 6].

dictions for cell tuning to gaze direction: (1) gaze direction should be important to STS cells; (2) when cells are tuned to both head angle and gaze angle the optimal angles for the two cues should coincide and (3) gaze direction should be more important than head view.

These predictions receive some confirmation from previous data. The majority (36 out of 56 tested) of the cells sensitive to head view were also sensitive to gaze direction (Perrett et al., 1985a). For all of these cells the preferred gaze direction was compatible with preferred head direction. That is, cells selective for the face view responded more to eye contact than to laterally averted gaze, while cells selective for the head turned laterally away from the monkey responded more to laterally averted gaze. Of even more relevance was the observation that sensitivity to gaze direction could overwrite sensitivity to head view (see below).

SENSITIVITY TO EYE CONTACT: ATTENTION DIRECTED TO THE VIEWER

Eighteen cells selective for the face view preferred eye contact to averted gaze. This is illustrated in Figures 3, 4 and 5 for cells sensi-
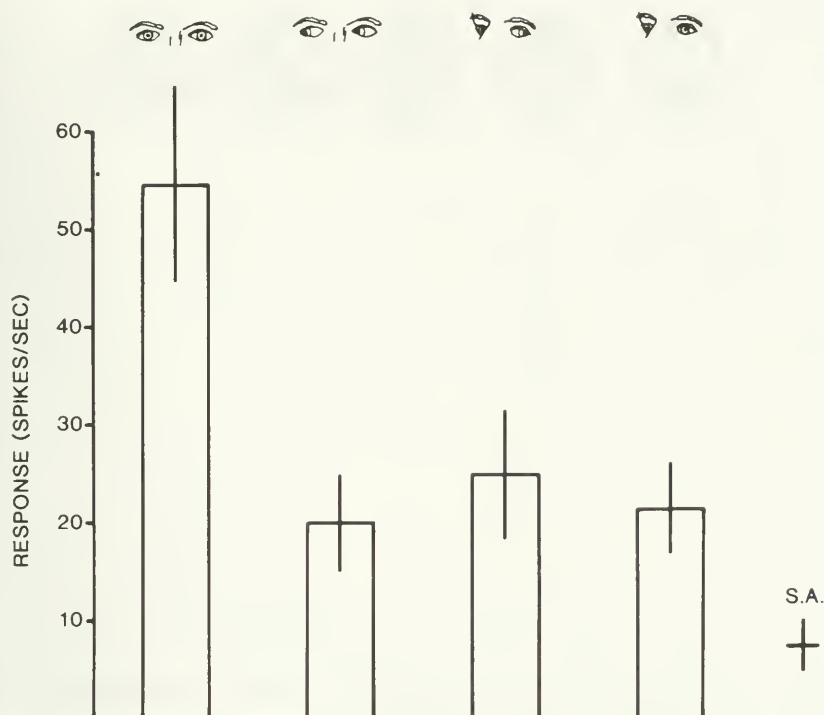
FIGURE 4. **Sensitivity to eye contact with the eyes viewed in isolation.** Upper: schematic representation of stimuli used for testing. Lower: mean and standard error of response of one cell (M047) to restricted views of the eye region. [N = 6, 6, 5, 4, 5].

tive to gaze direction in the vertical and the horizontal planes. For the cell illustrated in Figure 3 head view and gaze direction are independently important. With the eyes occluded by a bar the cell showed a preference for the full face view over the half profile view ($p<.05$, Newman-Keuls). Here the eyes are not visible so the discriminative response to head view must be based on other features of the head.

With the eyes visible and gaze aimed in different directions the cell was more responsive to eye contact for the full view than to other views with either the face or eyes averted laterally by 45° ($p<.05$, each comparison). In this instance the cell was selective for eye contact with only the full face view (overall effect of conditions: $F(6,29) = 7.2$, $p<.001$; number of trials per condition (N) = 6, 5, 4, 4, 3, 4, 6). A more common pattern of sensitivity was for cells to display a preference for eye contact for both views of the head (i.e., independent of head position in the horizontal plane). The pattern of eye gaze direction for this cell is replicated in a situation where only the eyes remain visible and the rest of the face is screened from view (Figure
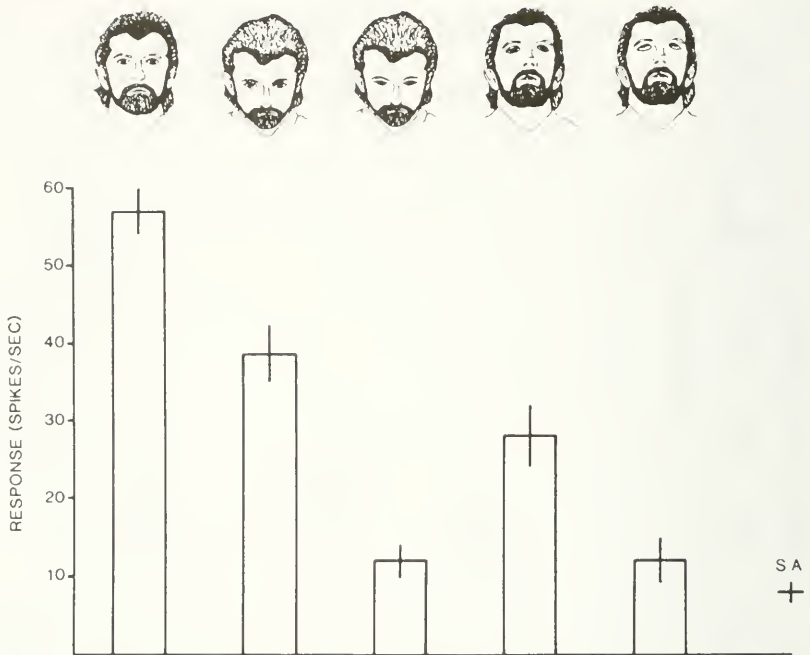
FIGURE 5. Sensitivity to gaze directed to the viewer in the vertical plane. Upper: schematic representation of stimuli used for testing. Lower: mean and standard error of response of one cell (P050) to the stimuli. [N = 5, 3, 7, 3, 6, 7].

4). The frontal view of the head with eye contact produced a response significantly greater than spontaneous activity and the responses to the face or eyes laterally averted ($p<.02$, each comparison; overall effect of conditions: $F(4,21)=6.1$, $p<.005$; N = 6, 6, 5, 4, 5).

Sensitivity to eye contact was also found for different head views in the vertical plane. This is illustrated in Figure 5 for a cell which responded more to the full face view than to the face rotated 45° up or down ($p<.05$, each comparison). For the head rotated up and down the cell was more responsive to gaze directed to the observer than to the same head views with vertically averted gaze (overall effect of conditions: $F(5,25)=40.8$, $p<.001$; N = 5, 3, 7, 3, 6, 7). For these latter views the eyes are also turned away from the observer. The cell's response to head up and head down was augmented when eye contact was made ($p<.05$, each comparison). The cell is, thus, selective for eye contact independent of the vertical orientation of the head. While the cell may have an overall preference for the full face view it would be erroneous to conclude that the sole function of the cell was to detect

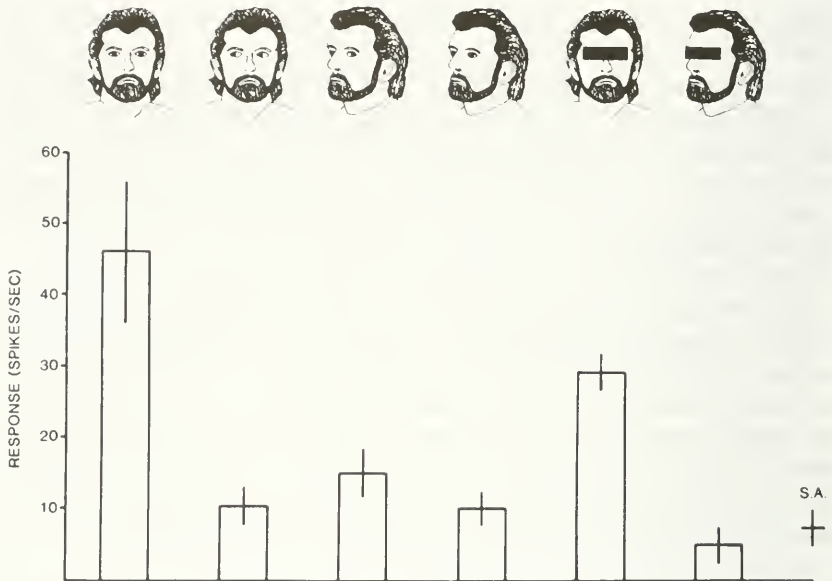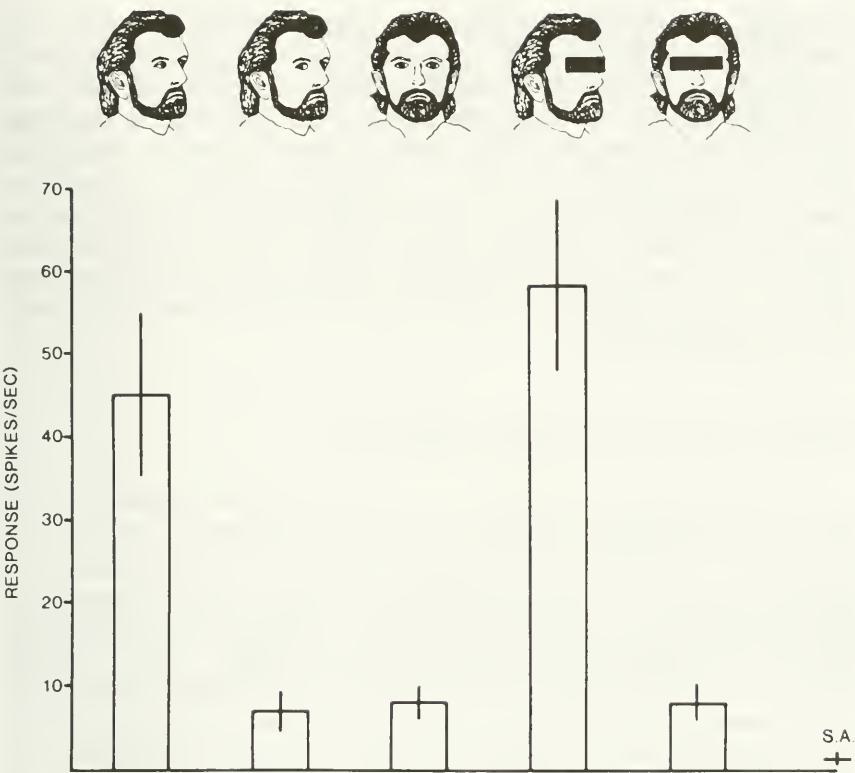**FIGURE 6. Sensitivity to head and gaze directed to the side.**
Upper: schematic representation of stimuli used for testing. Lower: mean and standard error of response of one cell (A086) to the stimuli [N = 6, 7, 7, 6, 5, 6].

the face view. The sensitivity to eye gaze is more consistent with a role in specifying attention directed at the observer.

ATTENTION DIRECTED LATERALLY AWAY FROM THE VIEWER

Many of the cells in the STS are sensitive to the head turned away from the observer in the horizontal plane. For some of these cells the preferred angle of view is one in which the head is turned away to such an extent that the eyes are not visible. For other cells with preferred views closer to the full face it was possible to examine the sensitivity to laterally averted gaze. Eighteen cells selective for the head turned away from the monkey also responded more to laterally averted gaze.

The cell illustrated in Figure 6 responded more to the head

turned 45° away from the monkey than to the full face view ($p<.001$). This difference between head views was also found with the eyes covered ($p<.001$). With the face and eyes visible the cell responded more to the half profile view with laterally averted gaze than to the same head view with eye contact ($p<.001$) (overall effect of conditions: $F(5,31) = 15.4$, $p<.0001$; $N = 6, 7, 7, 6, 5, 6$). Covering up the eyes does not eliminate the response and therefore the cell must be assumed to be sensitive to other regions of the profile. With the half profile view the response is depressed when the gaze is directed to make eye contact. The cell is thus sensitive to lateral aversion of both the eyes and the head.

DEFAULTING TO HEAD VIEW SENSITIVITY

There may be circumstances in which the gaze direction is not too clear. For example with strong lighting from above, the eyebrow ridges can cast a shadow over the eyes. In this case, the direction of attention can still be analysed (though perhaps with less certainty) from the direction in which the head is pointing. In these circumstances head angle could provide a useful "default." Cells showing combined sensitivity to the full face view (with the eyes occluded) and to eye contact (e.g., Figure 3) would thus be useful for signaling attention directed at the viewer in a variety of viewing conditions. Similarly, cells sensitive to both the profile view and averted gaze (e.g., Figure 6) would be useful for specifying averted attention under different lighting, etc.

ATTENTION DIRECTED UP OR DOWN

As mentioned above, sensitivity to head rotated away from the observer in the horizontal and vertical direction tended to be coded by separate cells. So too did coding of vertically and horizontally averted gaze. With gaze directed upwards, the cell in Figure 7 responded more to the face and to the face rotated upwards than to the same views with the eyes directed to make eye contact ($p<.02$). The cell also responded more to the profile turned upward than to the profile viewed in its normal orientation ($p<.02$) (overall effect of conditions: $F(7,36) = 17.6$, $p<.0001$; $N = 8, 4, 5, 6, 3, 7, 4, 7$). The cell is not simply coding head or eyes "turned away" since it does not respond to the profile face or to the face rotated downward.

If it is assumed that the function of the cell's responses is to provide an indication that another individual is directing attention to some place in the air, above the observer's head, then other aspects of
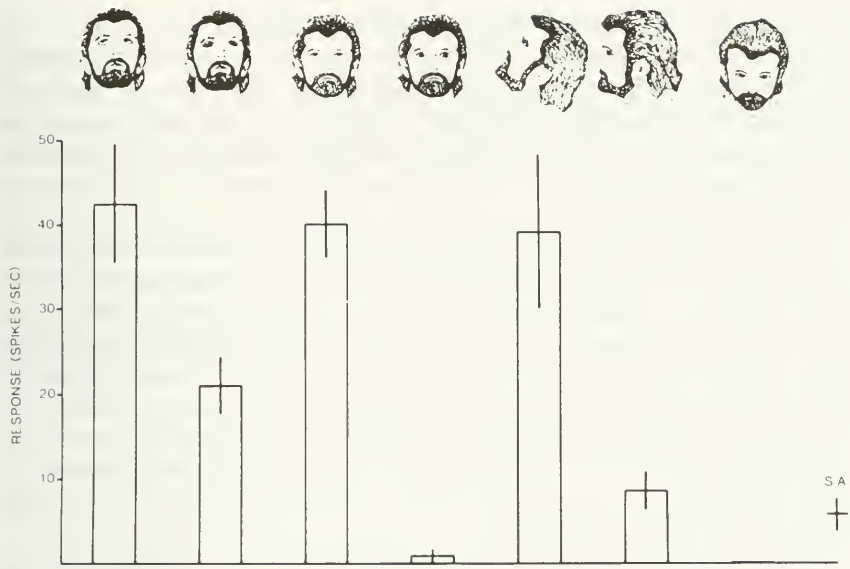
FIGURE 7. Sensitivity to head and gaze directed up. Upper: schematic representation of stimuli used for testing. Lower: mean and standard error of response of one cell (A078) to the stimuli. [$N = 8, 4, 5, 6, 3, 7, 4, 7$].

the cell's response make sense. While the cell does not respond to the full profile in its normal orientation, it does respond to the profile rotated upwards. The upward pointing profile would indicate that the individual being viewed is directing attention upwards.

When we consider gaze direction it is notable that the cell is unresponsive to both the full face and the face rotated upwards when the gaze is directed to make eye contact with the observer. For these stimuli the gaze angle gives a good indication that attention is not directed upwards but is directed at the observer. On the other hand, the cell does respond to both the full face view and the face turned upwards when the eyes are raised upward. Thus the cell responds to the sight of eyes raised upwards independent of the head view.

OBJECT CENTRED ANALYSIS

Gaze direction and head view can be analysed with different frames of reference. There are three main reference systems potentially applicable here (Feldman, 1985). These are the viewer, the object or individual under observation, and some part of the environment. Using the viewer or part of the environment as frames of

reference to interpret the cell's selectivity provides simple accounts of the function of the cells. A cell preferring head up may be coding attention above the viewer or attention in the upper part of the environment. A cell preferring left profile may be coding attention to the viewer's left or attention to a point in the environment (that happens to be on the viewer's left). We have yet to determine which description is more applicable.

Using the object as a frame of reference (an object centred analysis) is more complicated and appears less applicable to the results. This analysis utilizes the principal axis of the object or individual under observation as the frame of reference (Marr & Nishihara, 1978; Marr, 1982). For the cell (in Figure 7) responding to the face or profile with head raised, the angle of the head can be referenced to the torso. Under this scheme one might interpret the cell's activity as coding neck extension; the cell responding to all views of the body where the neck is extended away from the chest. This account does not explain the sensitivity to gaze direction.

For the same cell, attempts to relate the direction of gaze to the head viewed (also an object centred analysis) fail to produce a consistent description of the selectivity for gaze with different head angles. For the head level the cell responded well to the eyes directed upwards in their sockets but not to the eyes in the mid position of their sockets looking straight ahead. One might therefore conclude that the cell is coding eyes upward in their sockets. This account fails for two reasons. Firstly, the eyes in their mid socket position worked well when the head was raised. Secondly, the account predicts that the head lowered with direct eye contact (a posture commonly used as a threat signal) should activate the cell, since the eyes would be directed upwards in their sockets and would make eye contact with the observer. The cell, however, failed to respond to this configuration (data not illustrated).

DISCUSSION OF SENSITIVITY TO HEAD POSTURE AND GAZE DIRECTION

It is clear that the cells in the STS can supply information about the relative orientation of the head with respect to the viewer. The coding seems to be along two dimensions, corresponding to the degree of rotation towards or away from the observer in the horizontal and vertical planes. These two axes of analysis correspond to those noted to be most important in the neuronal coding of limb and head articulation (Perrett et al., 1985b, 1990a, 1990b).

In earlier studies, cells seemed to be insensitive to mirror reflection, responding equivalently to left and right profiles. Our more re-

cent studies indicate that a large number of cells are sensitive to the difference between mirror images and are selectively responsive to the head turned some angle laterally away from the viewer to one side only (Perrett et al., 1990b). [The left and right views of a real head may be slightly different but selective responses can be found with left and right mirror images of the same photographic slide (Perrett et al., 1989a, 1989c)]. Such left/right specificity is necessary if the function of the cells is to analyze direction of attention. By contrast, the separate coding of left and right profile views is unnecessary for object recognition because these mirror images have very similar visual characteristics.

In the vertical plane the majority of coding appears to generalize across different perspective views in the horizontal plane. As we have previously suggested, such generalization could be formed by the convergence of outputs of several different cells, each tuned to one horizontal view of the head with head raised posture. Indeed, such a convergence of information would seem to be a logical necessity since the visual cues defining head up posture are different for the face, profile, and back views. Some evidence in favour of this hierarchical scheme comes from the finding of a few cells that respond only to the head down from one view in the horizontal plane, e.g., left profile view with the head down.

The generalization of coding for head up or head down across a range of horizontal views of the head is interesting. The functional significance could reflect the fact that if an observer wants to direct his/her own attention to the point that another individual is attending, then all views with the head (and eyes) raised need the same behavioural response. If the observer sees a face turned up or a profile turned up or even the back of an individual's head turned up, then in each case, the observer needs to raise his or her own eyes to find what the other individual is looking at, or to what the individual is attending. Similarly, sight of a head (and eyes) down whether seen from the front, side, or back indicates a focus of another individual's attention in some lower part of the visual field.

The functional interpretation based on analysis of where an individual's attention is directed also accounts for the independent sensitivity to head posture and gaze direction displayed by some cells. Cells preferring the face turned to the observer also preferred the eyes to be turned towards the observer; cells preferring a laterally averted head posture also preferred laterally averted gaze and cells preferring a head posture raised in the air also preferred gaze directed upwards.

From the various populations of cells responsive to the sight of the head, the STS can code head posture and gaze direction of other individuals. These cellular mechanisms could have a role in social

behaviour. We have argued that one important function of the cells is to provide information about the focus of attention of other individuals. They thus provide answers to the questions "is that individual looking at me?" and if not "to where in the environment is that individual attending?".

II. PREDICTING THE CONSEQUENCES OF ONE'S OWN ACTIONS: STUDIES OF POLYSENSORY UNITS IN THE TEMPORAL CORTEX

The same brain region containing cells responsive to faces also contains cells responsive to somatosensory stimuli. In the upper bank of the STS of anaesthetized macaque monkeys Gross and his colleagues (Gross et al., 1981; Desimone & Gross, 1979; Bruce et al., 1981) found that tactile receptive fields were very large, often covering the whole body. Responses to tactile stimuli were extremely sensitive (detecting the displacement of a single hair) but were not selective for the nature of the tactile stimulus. Responses were usually transient in nature and were nonhabituating. A high proportion of cells with tactile responses were also responsive to visual stimuli. Bruce et al. (1981) found that the visual responses of such bimodal cells occurred over extremely large receptive fields (often cells would respond to stimuli throughout the entire visual field). Different classes of visual responses were observed, the majority preferred moving stimuli but were unselective for the form of the moving stimulus.

As discussed in the first part of this paper, the upper bank of the STS is known from a number of studies to contain populations of unimodal visual cells which exhibit a very high degree of selectivity, responding only to the sight of heads, or particular body movements. The cells with selective visual responses are not uniformly distributed in the STS but exist in patches (Perrett et al., 1985a). This patchy organization of physiological properties may coincide with the patchy anatomical distribution of input and output connections with this region (Seltzer & Pandya, 1984; Harries & Perrett, 1989; & D.N. Pandya, personal communication). It is possible that selective visual neurons and unselective polymodal neurons exist in different patches within the same cortical area.

Given the high degree of visual selectivity exhibited by cells responsive to the head, the apparent lack of selectivity exhibited by the cells processing somatosensory information and visual motion is surprising. This discrepancy was the main motivation for the present study. We reasoned that a re-examination of somatosensory coding in awake, behaving monkeys might reveal selectivity in the processing which is not apparent in the anaesthetized state. Cells selective for visual stimuli in the upper bank of the STS (area TPO of Seltzer &

Pandya, 1978) are responsive to stimuli originating from other individuals. For example, cells selective for faces or body movements respond to the sight of faces and movements of other individuals. The visual processing could be construed as providing information useful in social or predator/prey interactions.

SOMATOSENSORY PROCESSING

Somatosensory processing in TPO could be signalling the presence of others in the same way as visually responsive cells. In anaesthetized monkeys all stimulation is derived passively from other individuals (the experimenters). This reasoning led us to investigate what would happen in the awake, behaving state when the monkey actively caused the tactile stimulation by, say, touching itself.

With anaesthetized monkeys it is only possible to measure the effect of "passive" tactile stimulation, that is, stimulation which does not arise "actively" through the monkey's own movements. Such passive stimulation, when conducted out of sight, is inherently unpredictable in nature. In the awake behaving state, active tactile exploration (out of sight) can lead to both predictable and unpredictable stimulation. Encountering a familiar object in a familiar location (for example, one's own body surface) produces predictable sensations, whereas encountering objects which have been placed within reach without one's knowledge produces unpredictable sensations.

During the investigation it became apparent that STS neurons were dependent on whether stimuli could be "expected." Neurons discharged to somatosensory stimuli only when stimulation was unexpected. A study was therefore made investigating the relationship between the activity of the neurons and the predictability of the tactile stimulus based on other sources of tactile or visual information. The results of the study have been described in brief (Mistlin et al., 1986; Chitty et al., 1986; Perrett et al., 1989d) and are the subject of a fuller report (Mistlin & Perrett, 1990).

METHODS

As explained above, passive stimulation out of sight is unpredictable and unexpected. We arranged unexpected active stimulation to occur by placing novel textures (wood, fur, metal) on some part of the primate chair which the monkey frequently explored (e.g., the foot perch), or in some part of space that the monkey would encounter during its movements. Tactile stimulation out of sight was also compared to stimulation in sight with the monkey able to see the object causing tactile contact.
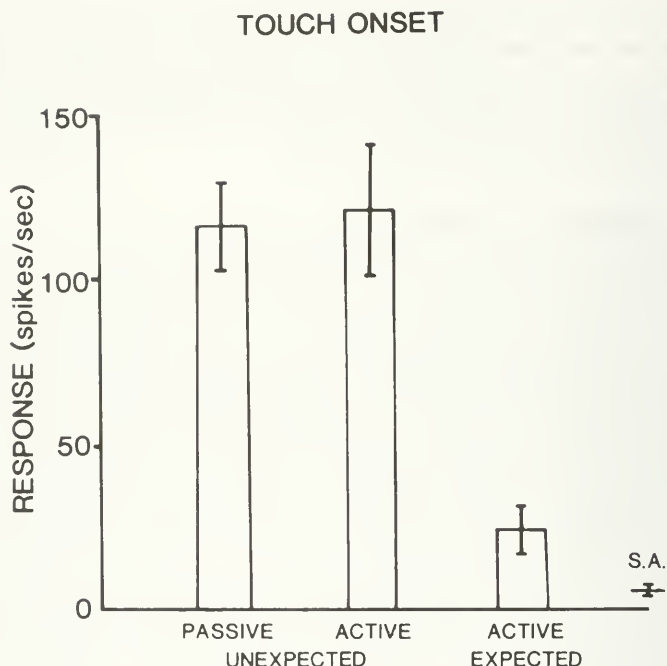
FIGURE 8. Comparison between response to expected and unexpected tactile stimulations. The mean and standard error of response is illustrated for one cell (F026). $N = 5, 5, 6, 8$.

RESULTS

Tactile Stimulation out of Sight

Testing with passive tactile stimulation revealed results that were similar to those obtained in the anaesthetized state. We found that cells responsive to somatosensory stimuli had very large receptive fields covering most of the body. The cells also displayed an apparent lack of stimulus selectivity responding to tactile contact with any stimulus (wood, fur, metal, etc.).

Figure 8 illustrates the results for one cell typical of those studied. It gave a large response when the monkey was touched by the experimenter (passive touch). Here the stimulation was inherently unpredictable. By contrast the cell was completely unresponsive when the monkey touched itself or a familiar part of the primate chair (active touch) (overall effect of conditions: $F(3,20) = 32.6$, $p<.01$; $N = 5, 5, 6, 8$). Differences between responses to active and passive

stimulation can not be accounted for in terms of differences in pressure or area of skin stimulated because careful attention was given to ensure that stimulation was comparable. Furthermore, the cell responded to touch across a range of tactile pressures and across a range of positions over the body.

The monkey's own movements can also lead to unexpected stimulation. When the monkey explored the environment out of sight and encountered a novel object, then tactile stimulation was unexpected and the cell illustrated in Figure 8 responded. Thus, the important dimension was whether the stimulation was predictable and not whether the stimulation was active or passive.

Eighty-five cells were studied with expected and unexpected tactile stimulation arising actively or passively. The majority of cells (94%) did not respond above spontaneous activity when the monkey touched itself or any familiar part of the chair but were responsive when the monkey touched unexpected surfaces or was touched unexpectedly by the experimenter.

What is remarkable is that at the level of the primary sense organs, sensations arising from expected and unexpected surfaces could be identical, yet the STS cells respond only to unexpected sensations. For example, the monkey's paw touching fur at an unexpected place and the monkey touching its own leg would produce very similar somaesthetic stimulation of the skin, yet STS cells responded only to the former stimulus.

The generality of response to passive tactile stimulation with any type of material can mislead one into thinking that the somatosensory processing in the STS does not discriminate texture. The activation of somatosensory cells in the STS must depend on a mismatch between the tactile qualities of the surfaces that the monkey expects to encounter and the tactile qualities which actually arise at a given position. The fact that the cells do not respond to the tactile contact of an expected surface means that the cells (or mechanisms antecedent to them) have processed the physical properties of the surface (texture and hardness) and found them to match expected properties. Thus, the cells are selective for tactile texture but selectivity is conditional on spatial position and expectation of the stimulus at that position.

Tactile Stimulation in Sight

All the testing described above was conducted out of sight and thus visual information could not be used by the monkey to make any intermodal predictions about the occurrence and nature of the tactile stimulation. We have compared the responsiveness of 30 cells to tactile stimulation in and out of sight. For passive tactile contact the majority of cells' responses (70%) were significantly reduced when the

PASSIVE TOUCH ONSET
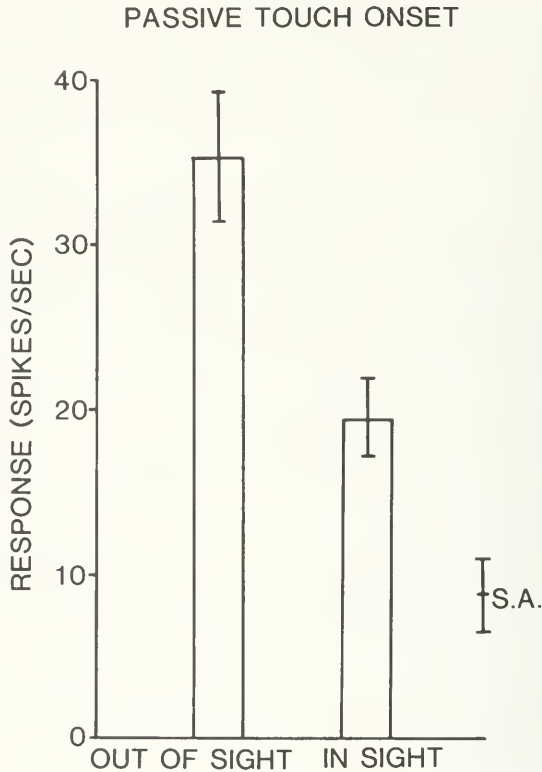
FIGURE 9. Comparison between passive tactile contact in sight and out of sight. The mean response and standard error of response for one cell (F123A) is illustrated for different conditions. $N = 10$.

monkey could witness the trajectory of an object moving on a course which resulted in tactile contact, as compared with an equivalent tactile contact from unseen objects at the same location on the skin (Figure 9; $p < .05$, each comparison; overall effect of conditions: $F(2,17) = 78.7$, $p < .01$; $N = 10$). The remaining 30% of the cells responded without difference to tactile stimulation in and out of sight.

A similar effect of vision was found for active tactile stimulation — with cells being more responsive when the monkey's movements resulted in tactile contact with objects that were out of sight, as compared with equivalent tactile contact with the same objects that were visible.

Novelty

The cellular sensitivity to the expected/unexpected dimension in stimulation does not reflect sensitivity to novelty per se, since cells

showed little if any short term habituation. Thus cells responded consistently to passive stimulation over 10-50 consecutive repetitions (interstimulus interval = 2-5 s). Similarly for active stimulation, repeatable responses were obtained during repeated exploration of unexpected surfaces.

If an object remains in the immediate environment long enough, then at some stage it may come to be regarded as familiar and hence predictable. We have, however, not yet investigated the full time course of this transition in status from unexpected to expected.

WITNESSING ONE'S OWN MOVEMENT

The distinction between expected and unexpected stimulation discussed above for the tactile modality can also be found in the visual modality. In the visual modality the distinction has a longer history of theoretical consideration. Sperry (1950) introduced an idea that the motor centres, when sending motor commands for moving the eyes, also send a corollary discharge to the visual centres to compensate for the retinal displacement during these voluntary eye movements. According to this theory, corollary discharges were not restricted to only visual stabilization mechanisms, but they functioned as a "central adjustor factor" to ensure perceptual stability during self-induced actions.

Von Holst and Mittelstaedt (1950) distinguished between "reafferent" stimulation arising as a consequence of one's own actions and "exafferent" stimulation which arises as a consequence of changes in the environment unrelated to one's own actions. Like Sperry (1950) they proposed that an "efference" copy of the motor commands to move the eyes is sent to sensory structures to null the reafferent stimulation which arises from the eye movement. In normal circumstances, the efference copy matches and cancels the reafferent stimulation, but this does not happen when, for example, the eye muscles do not move in accordance with the motor commands to move them. When the eye muscles are paralysed attempts to move the eyes to the right result in an unpleasant sensation where the visual world moves to the right (Hughlings-Jackson, 1932).

Note that the distinction between reafferent and exafferent stimuli is not quite the same as the expected/unexpected dimension described for the somatosensory modality. In different situations passive (exafferent) tactile stimulation can be either expected or unexpected (being touched in sight or out of sight). Similarly, there are situations in which active (reafferent) tactile stimulation is predictable or unpredictable (touch self or touch novel object out of sight).

In the visual modality exafferent stimulation is mainly unex-

pected and reafferent stimulation is mainly expected. This is particularly true in the case of eye movements where the consequent retinal changes are largely predictable. There are, however, many more situations where reafferent visual sensations are predictable; in a familiar environment retinal image motion caused by head and body movement is also predictable. Furthermore, the visual changes which arise as one's own limbs move into and within view are also largely predictable.

We have begun to study the responsiveness of movement-sensitive cells in the STS to the sight of the monkey's own limbs moving. This testing has again revealed the complexity of response sensitivity which at first glance appeared rather nonspecific. There are a variety of motion sensitive cells in the area TPO of the STS; many are form-selective and respond only to the sight of particular body movements. Others, however, are not selective for form and respond to all objects moving independent of size and shape.

MOTION SENSITIVE CELLS UNRESPONSIVE TO SELF-PRODUCED MOTION

We have studied a variety of different types of motion-sensitive cells lacking form selectivity. These cell types were selective for movement upwards, movement towards the monkey, movement into view and movement in any direction. Since at the retinal level each of these classes of movement occurs when the monkey brings its hand to its mouth, a comparison can be made between reafferent stimulation (retinal image movement resulting from the monkey's own action) and comparable exafferent stimulation (retinal image movement resulting from the movement of some external object in the environment unrelated to the monkey's action).

So far in a study of 35 cells we have found 26 which discriminated self-produced movement from nonself-produced movement. These 26 cells responded well to the experimenter's hand being brought into view or to an object moved by the experimenter into view but were unresponsive to the sight of the monkey's own hand coming into view along the same trajectory. None of these cells which discriminated between movements of the experimenter's hand and the monkey's own hand, showed sensitivity to form, size, or velocity which could account for the difference in response. Indeed, the cells generalized their responses to movements of objects of different size, colour, etc. Nine cells studied showed no difference between the sight of self-produced movements and the sight of movements not produced by the monkey.

Figure 10 illustrates the responses of one cell sensitive to the
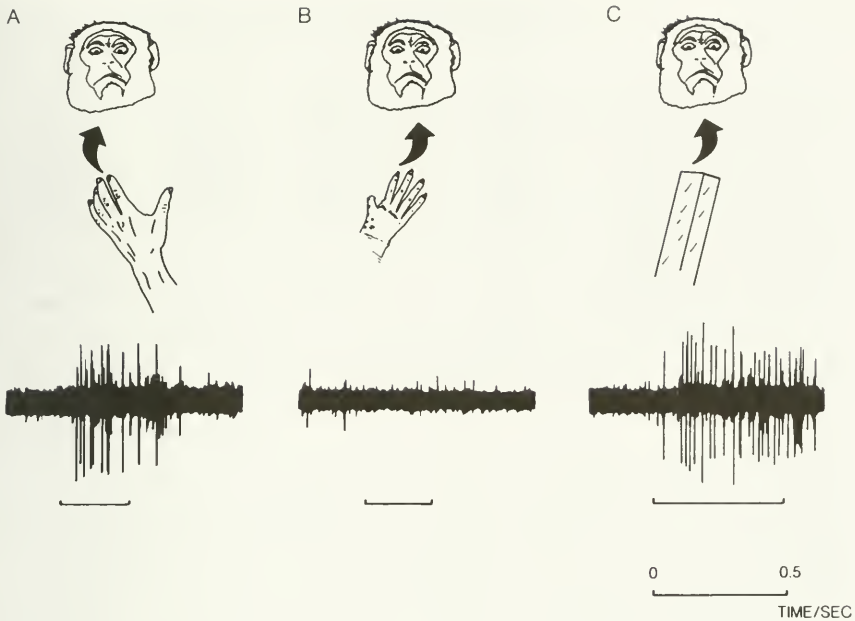
FIGURE 10. Motion sensitive cell unreponsive to the sight of own limb movement. Three trials with a human hand, the monkey's own hand, and a bar entering the field of view. Upper: stimuli illustrated schematically. Lower: traces of neuronal activity with the onset and duration of the moving stimuli marked by the horizontal line.

sight of stimuli moving upwards and into the field of view. This cell displayed a lack of form selectivity, responding when small objects, large objects, and the experimenter's hand were brought into view. When, however, the monkey brought its own hand into view, with or without small pieces of food, there was no response above spontaneous activity.

One might assume that the difference in conditions reflects different states of attention — the monkey paying little or no attention to its own hand but looking at and attending to other objects coming into view. This explanation is unlikely, first because video film reveals that the monkeys pay acute attention to their own hands when they bring food towards their mouths. Second, we have found that responses to a moving stimulus (other than the monkey's hands) occur even when the monkey is not looking directly at this moving stimulus (Perrett et al., 1985a). Measurements of receptive fields of motion-sensitive cells both in the anaesthetized preparation (Desimone et al., 1984) and in the awake monkey (Perrett et al., 1989a, 1989b; Perrett, Harries, & McHugh, unpublished studies) reveal that they are extremely large, usually extending more than 20° from the
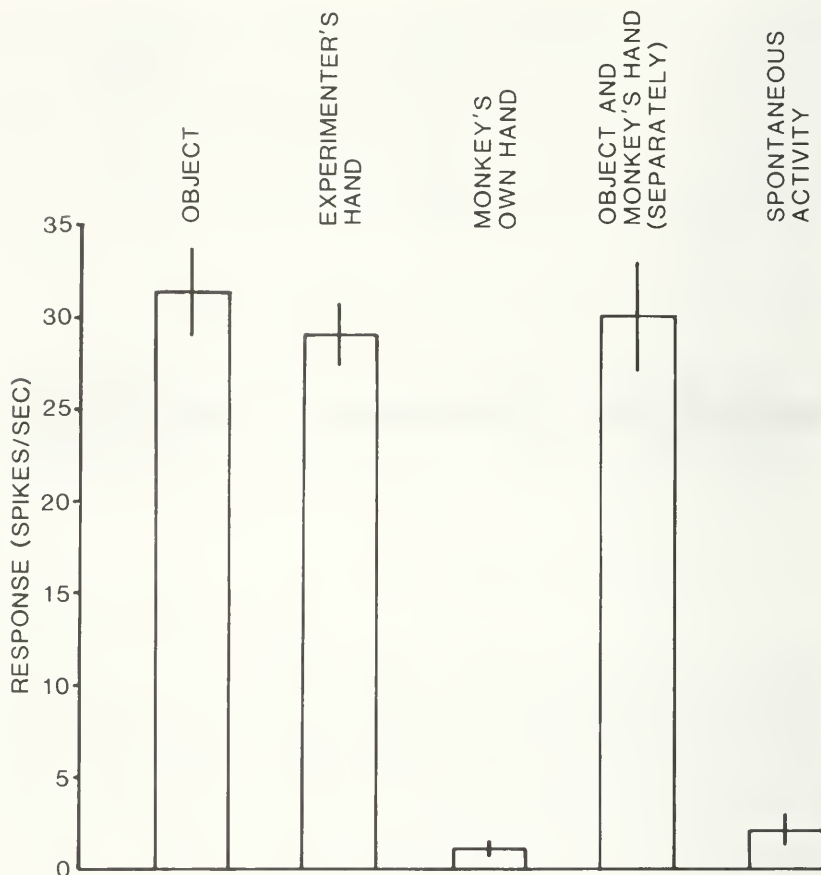
FIGURE 11. Quantitative comparison of self- and nonself-produced motion. The mean and standard error of one cell's responses are given to the sight of different stimuli moving into the field of view. $N = 14$.

fovea in all directions. Throughout these fields the cells are equivalently responsive to one type of movement. Thus, even if the monkey was not directly fixating on its own hand, one would still expect a neuronal response to hand movement because the movement would fall within the large receptive fields.

The absence of response to the monkey's own hand movement is not due to some general shut-down of motion processing during the hand movement. The cell illustrated in Figure 11 is more responsive to the sight of objects and the experimenter's hand moving into view than to the sight of the monkey's own hand moving into view or to spontaneous activity ($p<.01$, each comparison). The cell's response to objects moving into view was, however, unaffected by the simultaneous presence of the monkey's own hand in view (overall effect of conditions: $F(4,65) = 64.2, p<.01; N = 14$).

CAPACITIES NECESSARY FOR IGNORING THE
SELF-PRODUCED SENSATIONS

It is interesting to consider what information would be necessary in order to ignore one's own limb movements. The process may involve information about the predicted or felt (perceived) position of the limbs, the predicted trajectory, velocity and direction of limb motion and the visual appearance of the limbs plus whatever they may be carrying. We have just begun to explore the ability of visually responsive cells in the STS to ignore self-produced movements and have not yet defined how this happens. So far, our studies only provide physiological evidence that expectations generated from an individual's limb movements do influence sensory processing of the sight of those movements.

A similar diverse set of information is needed to account for the difference between expected and unexpected tactile sensations. The lack of response to expected tactile stimulation indicates knowledge of the spatial lay-out of the immediate space around the subject, knowledge of the tactile properties of all surfaces within this space, information about the current position, and predicted trajectory of limb movement.

At the most general level, an animal must be attuned to sensory events which indicate the actions of other animals but this can only be achieved by being able to ignore the sensory events which arise from the animal's own actions. The response properties of cells in the STS show that there are neural mechanisms sensitive to the predictable consequences of an individual's actions in the visual and tactile modalities. Predictable reafferent stimulation in visual and tactile modalities is effectively ignored by the majority of the neurons in the STS. This allows unexpected stimulation to be selectively detected.

The effect of expectation is not restricted to reafferent stimulation. Even with sensory information arising from changes in the environment that are unrelated to the monkey's own actions, we find that expectations set up on the basis of information from one modality can be used to null or attenuate processing of sensory information in a second modality. Hence the sight of an object moving on a course likely to contact the skin surface can attenuate the neuronal responses to the tactile stimulation at contact.

CONCLUSION

The three types of stimuli processed in the STS that have been discussed here have in common the fact that they are all potent in releasing orienting responses. Reflection on one's own experience makes this obvious. Faces, particularly those making eye contact are

extremely arousing stimuli. You soon become aware when someone is looking at you. Similarly, in the tactile modality it is very difficult to ignore a tactile stimulus that arises when someone or something unexpectedly touches you, whereas equivalent tactile stimulation arising when you touch yourself or some known surface goes largely unnoticed. Similarly we are not startled by the sight of movements of our own hands but we are likely to be alerted by other stimuli moving into view, particularly when these are close to our body.

Since unpredictable sensations often arise from other animals, the STS area appears well suited to defining sensory stimuli that are important in social or predator/prey interactions.

In general, sensory effects which are the predictable results of one's own actions do not need attention but (like faces) visual movements and tactile stimuli that are unexpected usually require behavioural reactions. The capacity to ignore self-produced sensations when they are predictable is a capacity which relies on an internal representation of the local environment from which to make predictions as to how sensory input from the environment will alter as a result of the organisms own actions. This type of assertion has frequently been suggested from psychological considerations (Gregory, 1980; MacKay, 1973) but as yet there has been little physiological evidence for the role of expectation and prediction in sensory information processing.

ACKNOWLEDGEMENTS

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PERCEPTION OF SPECIES-SPECIFIC VOCALIZATIONS BY ISOLATE-REARED BUDGERIGARS (*MELOPSITTACUS UNDULATUS*)

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ABSTRACT: Budgerigars were trained with operant conditioning procedures to discriminate among sets of calls from several species in a Same-Different task. Response latencies from this task were analyzed in several ways including multidimensional scaling (MDS) and cluster analysis. The pattern of response latencies from budgerigars reared in a large group of conspecifics was compared to that of budgerigars reared in acoustic and social isolation. Results show that budgerigars with previous experience with species-specific vocalizations and isolate-reared birds who had never heard such sounds can both discriminate among the categories of species-specific vocal signals. But, results from MDS and cluster analysis also show that rearing budgerigars in isolation has subtle effects on the perception of these categories of vocal signals.

INTRODUCTION

A major historical question in perceptual development is the extent to which natural perception categories are learned or innate (Gibson, 1969; Marler, 1982, 1984). This question takes on special significance for organisms that must learn their vocal signals by reference to an external auditory model (see, for example, Marler, 1987; Marler & Peters, 1989; Kuhl, 1989). Aside from humans, only birds (i.e., songbirds, parrots, and perhaps hummingbirds) have been shown to rely on learning to develop a vocal repertoire (Kroodsma & Miller, 1982).

Previous work shows that budgerigars (parakeets), when deafened as young, develop abnormal contact calls as adults (Dooling, Gephart, Price, McHale, & Brauth, 1987). Budgerigars reared in social and acoustic isolation from other birds also develop contact calls that fall outside the range of usual acoustic variation seen in this class of calls but the calls of isolate birds are not nearly as distorted

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as the calls of deafened birds (Dooling, Unpublished data). These kinds of experiments establish that hearing and an external auditory model are required for normal vocal development in budgerigars. The present experiments pose a different question about the role of auditory perception in vocal development. Do budgerigars who have never heard species-specific vocal signals perceive the various acoustic and functional categories of budgerigar vocalizations as experienced birds do? Or, does the perceptual grouping or clustering of complex vocal signals according to functional and acoustic categories require prior experience with the vocalizations in the appropriate social and communicative context?

METHOD

Animals

The experimental birds were nine adult budgerigars (*Melopsittacus undulatus*) obtained from a breeding colony at the University of Maryland. Following fledgling, seven of these birds (3 male, 4 female) remained in this colony of roughly 75-100 other budgerigars. Prior to experimentation, these birds were housed in large flight cages containing 10-15 other budgerigars in a large aviary. During experimentation, these birds were housed in pairs in small breeding cages. In the following experiments, we refer to these birds as normal birds.

Two isolate-reared birds (both male) were also observed. The isolate birds were in acoustic and social isolation in small animal sound isolation chambers (Industrial Acoustics Corporation) from the age of about 3 weeks and were tested beginning at the age of 8 months. These birds were housed in social and acoustic isolation during the conduct of these experiments. Yellow millet was used as reinforcer during experimental sessions and standard mixed parakeet seed was available during free-feeding times. The birds were kept on a normal photo-period correlated with the season and testing for all birds continued throughout the year.

Apparatus

The apparatus for training and testing the birds has been described elsewhere in detail (Dooling, Brown, Park, Okanoya, & Soli, 1987; Dooling, Park, Brown, Okanoya, & Soli, 1987). The birds were tested in small wire cages mounted in sound-attenuated chambers. One wall of the wire test cage was modified by the addition of a custom-built operant response panel constructed of two sensitive microswitches with light emitting diodes (LEDs) attached and a standard

pigeon grain feeder. One microswitch served as an observation key and the other as a report key. A bird could trip the microswitch by pecking at the LED. All experimental events were controlled by an IBM PC-AT microcomputer. Contact calls were stored in computer memory in digital form and output at a sampling rate of 20 kHz through D/A converters during a trial.

Training and Testing Procedure

Briefly, the birds were trained on a "Same-Different" task (Dooling, Brown, et al., 1987; Dooling, Park, et al., 1987). A trial began with the illumination of the LED on the observation key. A response on the observation key resulted in the presentation of two calls separated by 300 ms and the illumination of the report key. A response on the report key within 2 s following the presentation of two different calls was rewarded with a 2 s access to grain. On the other hand, responses on the report key following the presentation of two identical calls was punished with a 20 s timeout period during which all lights in the experimental chamber were extinguished. Each trial was followed by a 1 s intertrial interval and then by a new trial sequence starting with the illumination of the observation key LED. A new trial sequence was also initiated if the bird failed to respond during the 2 s report interval. The dependent variable in these experiments was the response latency to peck the report key as measured from the end of the second stimulus.

Previous experiments with both simple pure tones and complex vocalizations have established that a budgerigar's response latencies on "Different" trials in this task are highly correlated with the discriminability of the stimuli—longer response latencies occur when the stimuli being discriminated are more similar. In other words, in this paradigm, response latency can be taken as a reliable and valid index of stimulus similarity (Dooling, Brown, et al., 1987; Dooling, Park, et al., 1987). Before being tested on the contact calls in these experiments, the birds were all trained on the Same-Different task with simple pure tones of different frequencies. Once the birds attained the concept of same-different, they transferred quickly, often without any decrement in performance, to different stimulus sets composed of vocal signals.

In the following three experiments, the test stimuli consisted of sets of 10-14 different bird calls presented at a peak sound pressure level of 72 dB(A) measured at the bird's head. We tested birds in daily sessions until all possible pairwise combinations of the different calls were presented once, resulting in a complete matrix of response latencies. In addition, trials which involved the pairing of each call with itself (i.e., "Same" trials) were repeated so that there were equal

numbers of "Same" and "Different" trials in a filled matrix. In tests with a set of 10 stimuli, for example, a "filled" matrix consisted of one latency value in each "Different" or off-diagonal cell and the average of 10 latency values in each "Same" or diagonal cell. A filled matrix required 2N(N-1) trials where N is the number of stimuli in the set. Testing was continued until at least five complete matrices of response latencies were obtained. These matrices were then averaged to produce a final latency matrix from each bird for subsequent analysis.

Evidence that the birds were successfully discriminating among the stimuli in any particular set was obtained by comparing the response latencies on "Same" trials with those on "Different" trials. For all of the matrices from all of the birds used in the present experiments, response latencies in the off-diagonal cells (different trials) were always significantly shorter than response latencies in the diagonal cells (same trials). Although the dependent variable in these experiments was response latency, we also recorded percent correct and false alarm rates as a means of comparing the overall performance of the two groups of birds on the task. Typically, in these and other auditory perceptual experiments involving the "Same/Different" task, hit rate was over 80% while false alarm rate was generally below 25%.

At the end of testing, the latency values (recorded in centiseconds) from the individual matrices were subjected to a log transformation and a single matrix representing the average of all of the matrices was computed. This average matrix was then folded about its main diagonal by averaging the corresponding cell entries in the lower and upper half-matrices (i.e., A-B with B-A combinations) and discarding the values in the diagonals (i.e., latencies from "Same" trials). This resulted in a half-matrix of response latencies containing a single value for each comparison as required by the multidimensional scaling algorithm.

Data Analysis Procedures

The goal of these experiments was to determine whether budgerigars reared in acoustic and social isolation perceive complex, species-specific vocal signals differently than budgerigars reared in a large group consisting of other conspecifics. To this end, the data were analyzed in several ways.

Multidimensional Scaling.   Multidimensional scaling procedures find an arrangement of points (stimuli) in multidimensional space by maximizing the correspondence between interstimulus distances (proximities) and the similarity between stimuli based on error

scores, confusion indices, response latencies, or other similarity mea-
sures (Kruskal & Wish, 1978; Shepard, 1980). In these experiments,
the SINDSCAL (Symmetric *IN*dividual *D*ifferences *SCAL*ing) algo-
rithm and program were used to analyze the response latency ma-
trices. Individual differences scaling finds a common solution for a
number of matrices (e.g., individual birds) by allowing each dimen-
sion of the spatial representation to expand or contract independently
for each individual tested. Subject weights describe the importance of
each dimension for each bird and provide an indication of the vari-
ance in each animal's data accounted for by stimulus distances along
each dimension. Subject weights provide a basis of comparison among
the birds in the perception of these stimuli.

Cluster Analysis.   The final data matrices were also subjected to
a hierarchical cluster analysis. Cluster analysis also describes the
structure of similarity data but in the form of a dendrogram. Hier-
archical cluster analysis groups calls according to a Euclidean dis-
tance metric with more similar calls clustered at less-aggregated
levels of a hierarchy (Mezzich & Soloman, 1980). In the present ex-
periments, we used cluster analysis to confirm the existence of a clus-
ter or grouping of stimuli which emerged from MDS. The single den-
drogram produced for socially experienced birds and for isolate-reared
was accomplished by combining data across individuals. These group
dendrograms provide an accurate reflection of the differences between
these two groups of birds.

Category Discreteness.   In the present experiments, both MDS
and Cluster Analysis are used to show stimulus groupings. Since
these are fairly complicated statistical procedures, another intuitively
simpler measure was also developed to explore the differences be-
tween birds in the perception of stimulus categories. To obtain this
measure, the average response latencies to all possible pairs of stim-
uli drawn from within a category (i.e., the same categories as deter-
mined by MDS and cluster analysis) are shown by a simple t-test to
be significantly longer (more difficult to discriminate among) than
average response latencies to all possible pairs of stimuli drawn from
among the categories shown by MDS and clustering.

Percent Correct Responding.   Isolate-reared birds could be abnor-
mal in a number of ways some of which might be more directly re-
lated to performance in the operant task rather than perceptual capa-
bility. As a check on this possibility, we used the percent correct and
false alarm rate to calculate a d′ for each of the sessions for each bird.
These values were compared for socially experienced and isolate-
reared birds by an analysis of variance using a split-plot factorial
design. Due to the number of comparisons, we chose to use a signifi-
cance level of $p < .01$.

FIGURE 1. Sonograms of 14 calls drawn from the budgeriger vocal repertoire. Each call is from a different bird and given a letter designation (A-N). Time marker is 100 ms. Reprinted from Dooling, Park,

STIMULUS SPACE
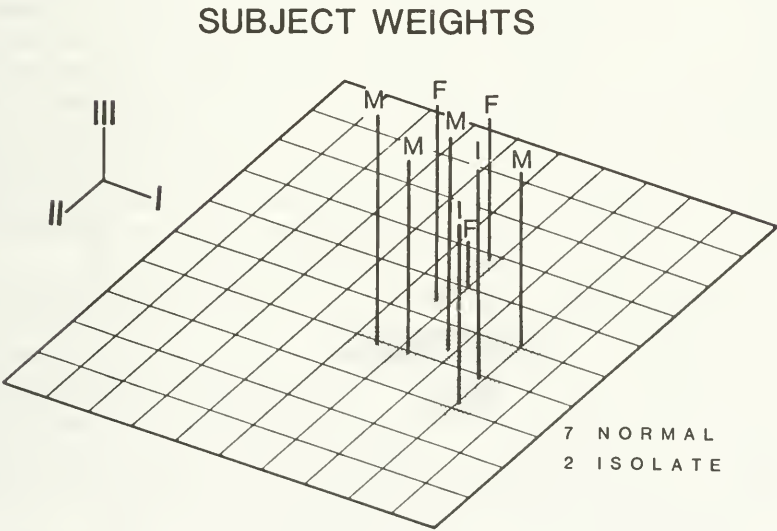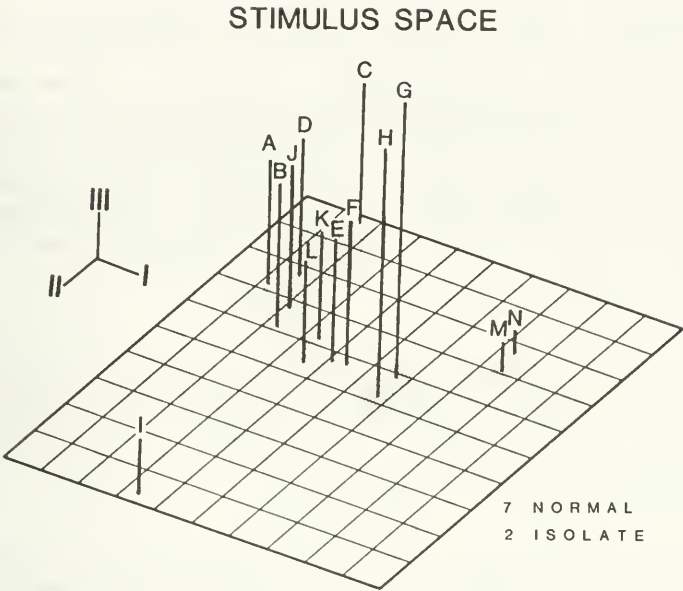
SUBJECT WEIGHTS

FIGURE 2 A. Three dimensional spatial representation of the perceptual similarity among 14 calls from the budgerigar vocal repertoire. Shading indicates perceptual categories as determined by a cluster analysis. B. Subject weights from the same solution.

EXPERIMENT 1: PERCEPTION OF NORMAL BUDGERIGAR CALLS

The budgerigar vocal repertoire contains a number of functionally and acoustically distinct call types. We have examined the perception of this set of calls by humans and budgerigars in an earlier report (Dooling, Park, et al., 1987). The following experiment compared the two isolate-reared budgerigars with socially-experienced budgerigars on the perception of these complex vocal signals.

Stimuli and Procedures

Four contact calls and two calls from each of the other major classes of vocal stimuli in the budgerigar vocal repertoire were used in this experiment. Sonograms of these stimuli are shown in Figure 1.

Results and Discussion

MDS and Clustering. The three-dimensional spatial representation generated by SINDSCAL of the perceptual similarity among these calls for the nine budgerigars is shown in Figure 2A. The distances in this solution accounted for 56.9% of the variance in response latencies with the first, second, and third dimensions accounting for 29.2%, 15.2%, and 12.6% respectively. The subject weights for this solution are shown in Figure 2B. The subject weights space shows that there are differences between male birds and female birds in the perception of these calls (as has been reported earlier for six of these birds in Dooling, Brown, Park, & Okanoya, 1990). But, the subject weights space also shows that isolate-reared birds are different from socially-experienced birds in the perception of these sounds.

The stimulus groupings are similar to those described earlier for both budgerigars and humans (Dooling, Park, et al., 1987). The results of a hierarchical cluster analysis on the average data matrix from the seven socially-experienced birds and the average data matrix from the two isolate-reared birds are shown as dendrograms in Figures 3 (Top and Bottom). Along with the differences in subject weights, the stimulus groupings obtained by a cluster analysis also show differences between normal and isolate-reared birds.

Category Discreteness. The within and between category latency comparisons reveal a similar pattern for both socially experienced and isolate-reared birds. For all birds, the response latencies to pairs of calls drawn from within categories were longer than the response latencies to pairs of calls drawn from between categories. These results are given in Table 1 as the log of the response latency (in centiseconds) times 100. Thus, a value of 150 in this table represents a "raw" or untransformed response latency of about 316 ms.
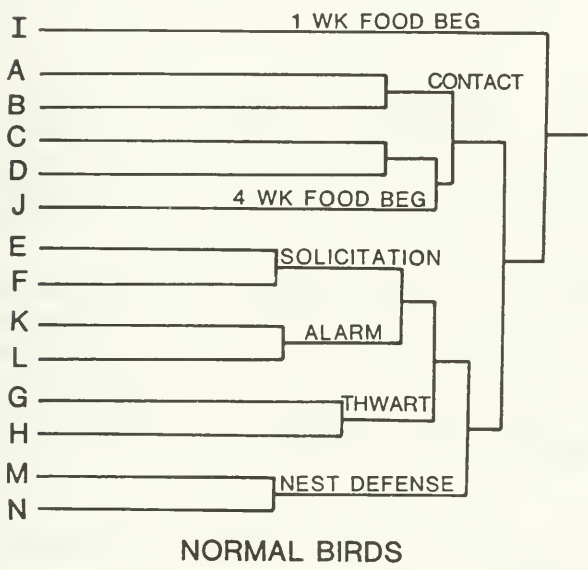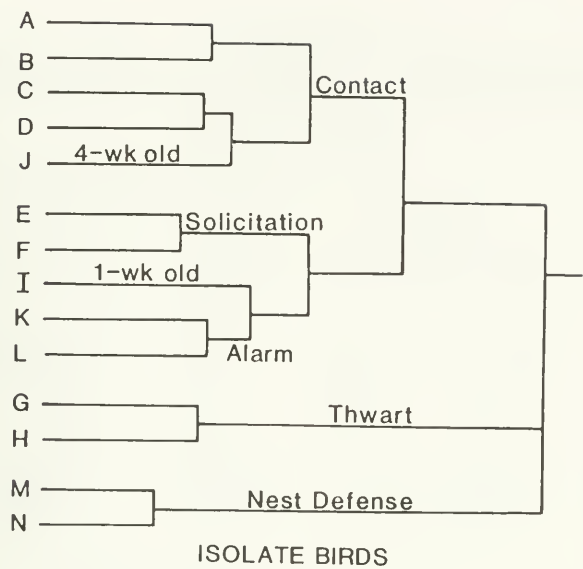
FIGURE 3. (Top). Dendrogram produced by a hierarchical cluster analysis on the latency data from two isolate-reared budgerigars discriminating among the set of 14 calls. (Bottom). Dendrogram produced by a hierarchical cluster analysis on the latency data for seven normal budgerigars.

TABLE 1

Comparison of Response Latencies (Log × 100) in Budgerigars Tested on Calls Drawn From Within and Between Categories (Assorted Calls)

| | Call Pairs Relative to Categories | | | | |
| | Within | | Between | | |
Animal	M	SD	M	SD	t(89)
	Normal Birds				
P8G	154	26.7	124	22.5	4.3*
P34	177	22.5	153	11.9	5.8*
P2Y	178	23.5	170	15.4	1.6
PRW	170	29.0	135	15.4	6.6*
P74	149	40.6	124	13.8	4.2*
P21	111	38.9	73	31.7	4.0*
P39	166	25.6	136	9.7	3.8*
	Isolate-Reared Birds				
PO2	153	32.8	118	13.0	7.0*
PO4	164	21.9	138	8.4	8.1*

*$p < 0.01$

Percent Correct Responding.   The results of a split-plot factorial design analysis of variance of d' values with two treatments (isolates vs. normals) and five repeated measures (sessions) failed to show a significant difference between isolate-reared ($M = 2.08$) and socially-experienced ($M = 2.65$) birds ($F(1,20) = 3.20$, $p > .01$).

The results of MDS show that isolation-rearing affects the perception of complex, species-specific vocalizations in spite of the fact that there was no effect in an overall measure of detection performance, d'. The results of cluster analyses also show that the stimulus groupings for isolate-reared birds are slightly different than those found for socially-experienced birds.

EXPERIMENT 2: PERCEPTION OF CONTACT CALLS OF OTHER SPECIES

The previous experiment shows that isolate-rearing affects the perception of species-specific vocal signals in budgerigars. The present experiment tests whether isolate-rearing affects the perception of a set of complex vocalizations consisting of three sets of distance calls: one set consisting of species-specific calls and the two other sets from
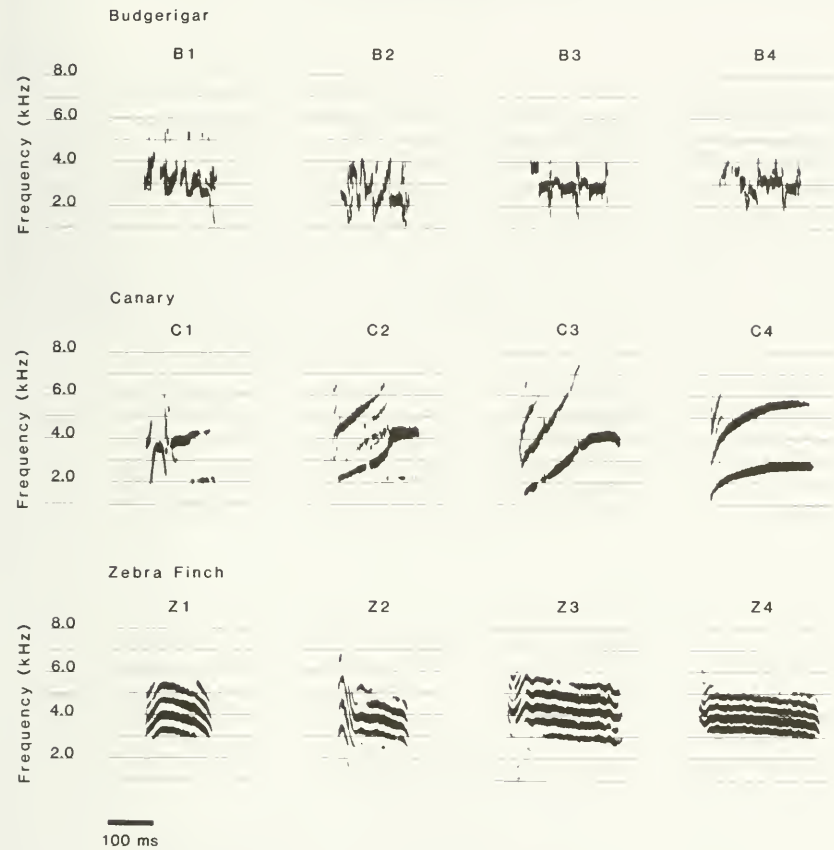
FIGURE 4. Sonograms of contact calls from four budgerigars, four canaries, and four zebra finches. Time marker is 100 ms. Reprinted from Dooling, Park, et al., 1987.

the canary (*Serinus canarius*) and the zebra finch (*Taeniophygia guttata castanotis*).

Stimuli and Procedure

The stimuli used in this experiment were contact calls from four budgerigars, four canaries, and four zebra finches. Sonograms of these stimuli are shown in Figure 4 and are identical to those used previously to test budgerigars (Dooling, Park, et al., 1987). The testing procedures were identical to those used in the previous experiment. All together, two isolate-reared birds and three socially experi-
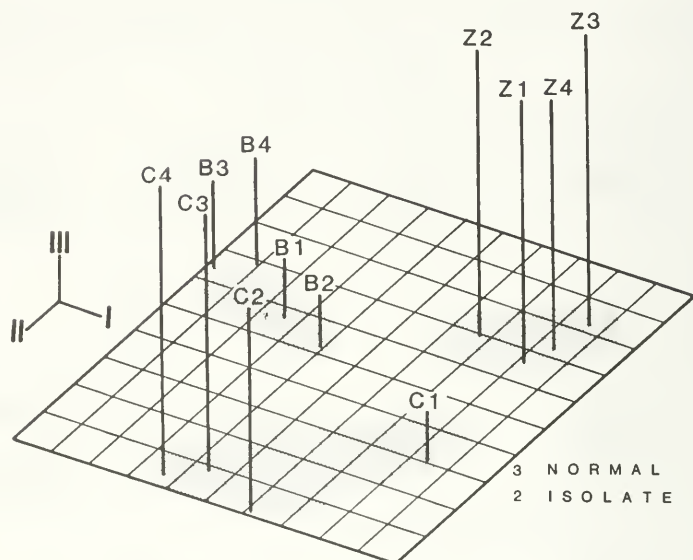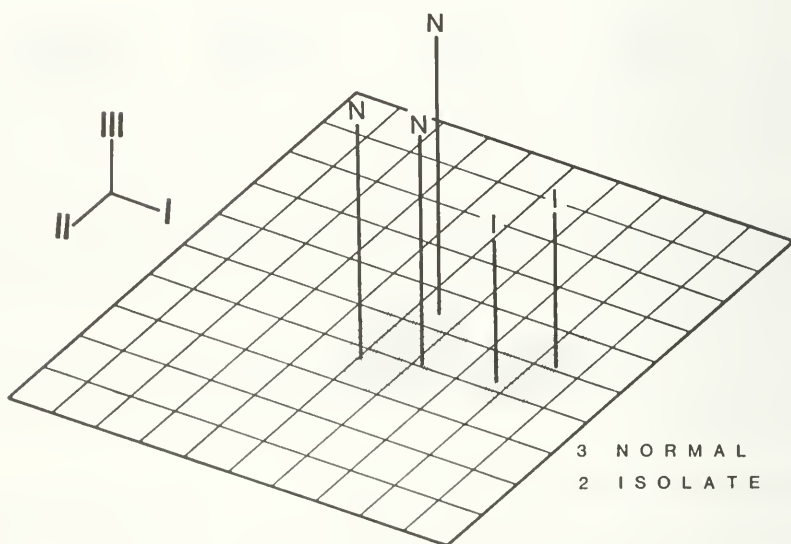
FIGURE 5 A. Three dimensional spatial representation of the set of mixed-species contact calls by three normal budgerigars and two budgerigars reared in acoustic isolation. B. The subject weights for this solution.

enced male budgerigars from the previous experiment were tested on this set of 12 mixed species contact calls.

Results and Discussion

MDS and Cluster Analysis.   The three-dimensional spatial representation by SINDSCAL of the similarities among these calls perceived by the five budgerigars is shown in Figure 5A. This solution accounted for 79.3% of the variance in the birds' response latencies with the first, second, and third dimensions accounting for 42.3%, 19.3%, and 17.7% respectively. The subject weights for this solution are shown in Figure 5B. As in the previous experiment, the subject
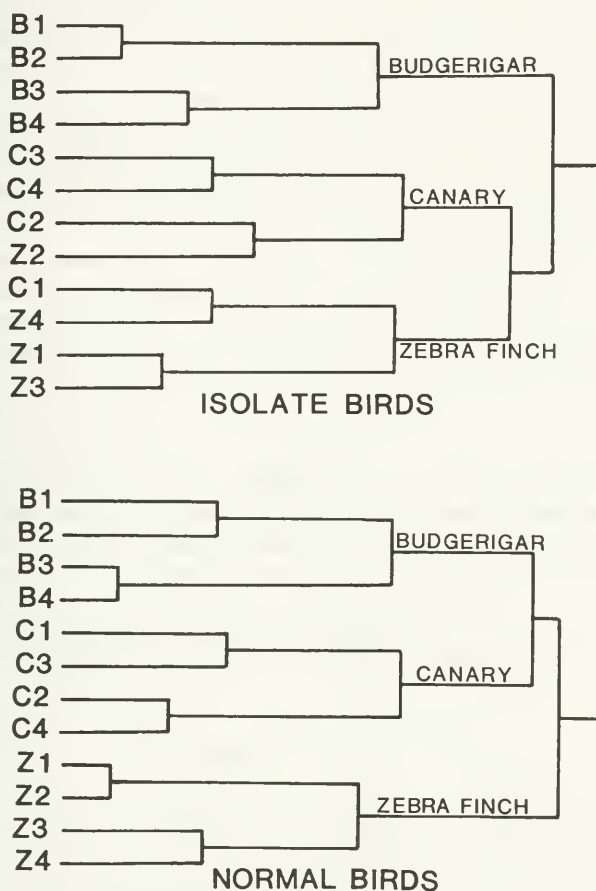
FIGURE 6 (Top). Dendrogram from the hierarchical cluster analysis of the latency data from isolate-reared budgerigars tested on mixed-species calls. (Bottom). Dendrogram from three normal budgerigars tested on same stimuli.

weights of isolate-reared birds are again separate from those of socially experienced birds.

The SINDSCAL solution for all the birds shows that the calls are grouped by species. The results of a hierarchical cluster analysis on the averaged data from isolate-reared birds and socially experienced birds are shown as dendrograms in Figures 6 (Top and Bottom). As in the previous experiment, there is a slight difference in the cluster dendrograms between these two groups of birds. Socially experienced birds group these calls by species. Isolate-reared birds show species-specific calls in one category but also show a slight intermixing of canary and zebra finch call categories.

Category Discreteness. The category-discreteness measure for both normal and isolate-reared birds reveals that the within category response latencies are significantly longer than the between category response latencies for all birds. These results (transformed values) are given for each of the five birds in Table 2.

Percent Correct Responding. An analysis of the d' values across birds also revealed no difference between the average d' of isolate-reared birds (M = 1.90) and socially experienced birds (M = 2.22) ($F(1,12) = 1.73, p > .05$).

These results parallel those of the first experiment showing differences in subject weights as well as differences in cluster dendrograms between isolate-reared and socially experienced budgerigars. These differences were found despite no statistical differences be-

TABLE 2

Comparison of Response Latencies (Log × 100) in Budgerigars Tested on Calls Drawn From Within and Between Categories (Mixed Species Calls)

| | *Call Pairs Relative to Categories* | | | | |
| | *Within* | | *Between* | | |
Animal	*M*	*SD*	*M*	*SD*	*t(64)*
	Normal Birds				
P21	152	22.1	119	8.1	9.0*
P74	130	18.9	104	9.1	7.7*
PRW	166	22.2	127	12.6	9.0*
	Isolate-Reared Birds				
PO2	149	16.6	124	8.1	8.4*
PO4	140	12.6	122	9.0	6.4*

*$p < 0.01$

tween these two groups in overall detection performance as measured by an ANOVA of d' measures.

EXPERIMENT 3: PERCEPTION OF ABNORMAL CONTACT CALLS

The previous experiments show that isolate-reared budgerigars, though different from socially experienced birds, can discriminate among several biologically-relevant classes of vocalizations which make up the species repertoire and among calls from different species of birds. This experiment was designed to test a more difficult discrimination involving budgerigar contact calls from normal budgerigars, isolate-reared, and deafened budgerigars. Calls from deafened budgerigars are abnormal and even sound abnormal to human listeners while calls of isolate-reared budgerigars, though still abnormal, tend to more closely approximate those of normal budgerigars (Dooling, Park, et al., 1987; Dooling, Gephart, et al., 1987; Dooling, Unpublished Data). The present experiment addresses the question of whether isolate-reared budgerigars perceive the calls from deafened and isolate-reared birds as distinct from those produced by normal budgerigars.

Stimuli and Procedure

The stimuli used in this experiment were contact calls from 10 budgerigars. Sonograms of this set of stimuli are shown in Figure 7. The set consisted of contact calls from two deafened birds, from six birds with normal hearing and social development, and one each from the two birds reared in acoustic isolation. This stimulus set also had been used in previous tests of budgerigar perception (Dooling, Park, et al., 1987). The testing procedures were identical to those used in the previous two experiments. Three male budgerigars from Experiment 1 and the two isolate-reared budgerigars used in both Experiments 1 and 2 were tested on this set of 10 contact calls.

Results and Discussion

MDS and Cluster Analysis.   The two-dimensional spatial representation of the perceptual similarity among the 10 contact calls for the five budgerigars is shown in Figure 8A. A two-dimensional solution was used in this case because the third dimension did not improve the variance accounted for by an appreciable amount. The subject weights corresponding to this solution are shown in Figure 8B. The total variance in response latencies accounted for by this spatial solution is 59.7% with the first and second dimensions accounting for

CONTACT CALLS

FIGURE 7. Sonograms of calls from normal, deafened and isolate-reared budgerigars. Time marker is 100 ms. Reprinted from Dooling, Park, et al., 1987.
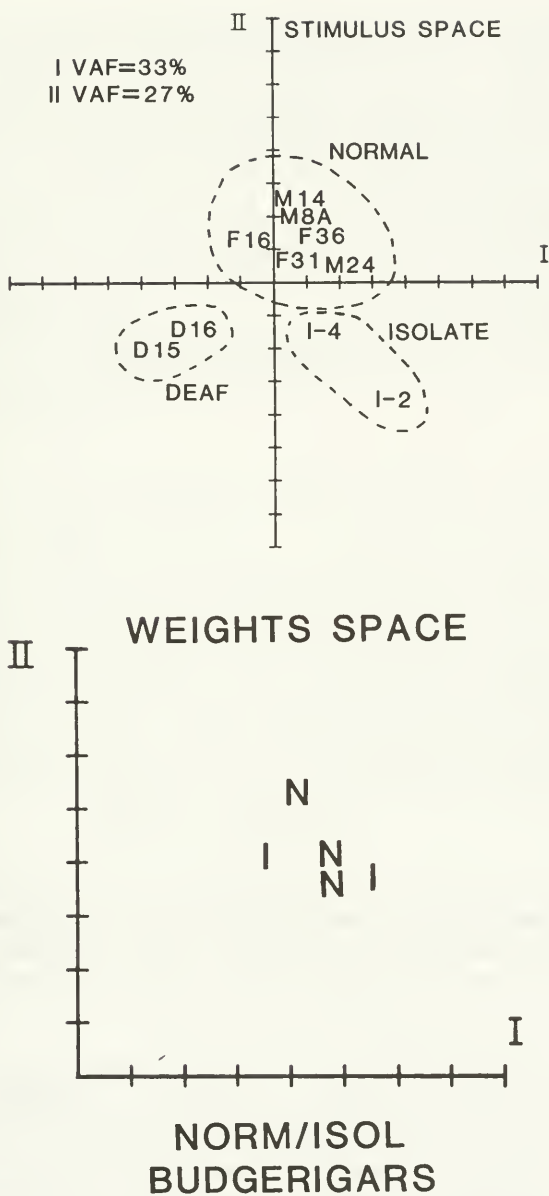
FIGURE 8 A. Two dimensional spatial representation of perceptual similarity among calls from deafened, isolate-reared, and normal budgerigars for all three normal and two isolate-reared budgerigars. B. Subject weights for the same solution.
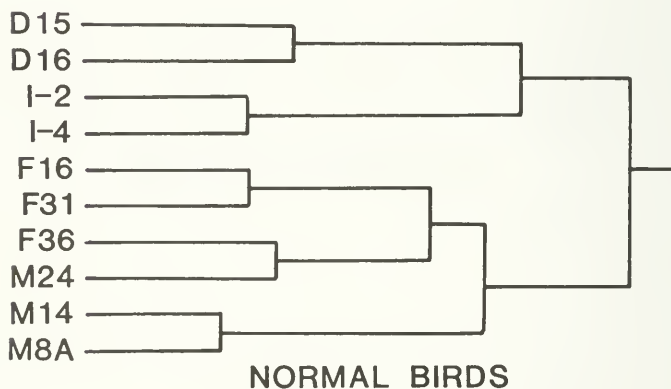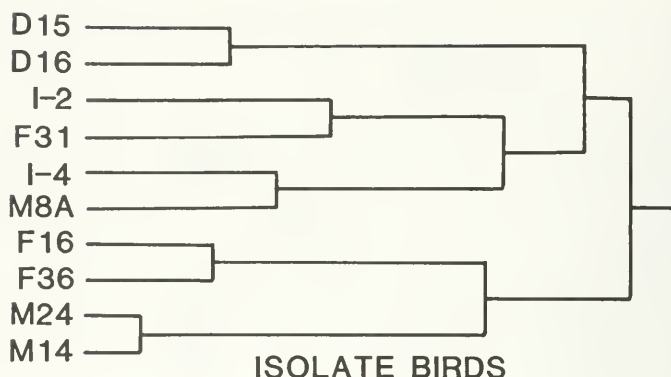
FIGURE 9 (Top). Dendrogram from a hierarchical cluster analysis of data from isolate-reared budgerigars tested on contact calls from deafened, isolate-reared, and normal birds. (Bottom). Dendrogram from three normal budgerigars tested on the same stimuli.

33.1% and 26.6%, respectively. The subject weights space reveals no systematic difference between normal birds and isolate-reared birds.

The results of a hierarchical cluster analysis on the averaged data from socially experienced birds and from isolate-reared birds are shown as dendrograms in Figures 9 (Top and Bottom). By this analysis, there are differences between the two groups of birds. Socially experienced birds show three clusters of calls corresponding to the calls of deafened, isolate, and normal birds. The clusters for isolate-reared birds show an intermixing of calls from socially experienced birds with those from the two isolate-reared birds.

Category Discreteness.   On the category discreteness measure for isolate-reared and socially experienced birds, within category laten-

cies are longer than between category latencies for all birds. These latencies (transformed) are given in Table 3.

Percent Correct Responding. The results of an analysis of d′ values across birds revealed no significant difference in the average d′ values between isolates ($M = 2.01$) and socially experienced birds ($M = 2.85$) ($F(1,12) = 3.85$, $p > .05$).

Thus, by a cluster analysis, isolate-reared budgerigars differ from normal birds in the perceptual grouping of stimuli. However, on the basis of subject weights from an MDS analysis as well as overall detection performance, isolate birds are not systematically different from normal birds. In aggregate, then, the differences between isolate-reared and socially experienced budgerigars in this experiment are probably quite small.

DISCUSSION AND CONCLUSION

In previous experiments on budgerigars, we developed a combination of operant conditioning procedures and multidimensional scaling and hierarchical clustering analyses to assess the perception of species-specific vocal signals (Dooling, Brown, et al., 1987; Dooling, Park, et al., 1987). These earlier findings showed that budgerigars, and indeed even humans, tested on calls from different species or on call exemplars from different classes of calls in the budgerigar vocal

TABLE 3
Comparison of Response Latencies (Log × 100) in Budgerigars
Tested on Calls Drawn From Within and Between Categories
(Abnormal Calls)

| | Call Pairs Relative to Categories | | | | |
| | Within | | Between | | |
Animal	M	SD	M	SD	t(43)
	Normal Birds				
P21	139	12.6	116	9.8	6.9*
P74	132	7.7	118	11.2	4.6*
PRW	166	15.4	144	14.0	4.9*
	Isolate-Reared Birds				
PO2	145	10.7	127	14.4	4.3*
PO4	152	19.3	135	8.8	6.4*

*$p < 0.01$

repertoire, show perceptual groupings or clusters that follow closely from what an acoustical and functional analysis of the calls would suggest.

In the three experiments reported here, we extend these previous findings, using the same stimuli, to budgerigars reared in social and acoustic isolation. Both socially experienced and isolate-reared budgerigars could discriminate among these complex vocal signals and there were no differences between the two groups of birds on an overall measure of detection performance, d'. Moreover, we knew from previous experiments that these stimuli form perceptual categories for budgerigars (Dooling, Brown, et al., 1987; Dooling, Park, et al., 1987). In each of the three present experiments both socially experienced and isolate-reared budgerigars showed longer response latencies to discriminate between pairs of stimuli drawn from within categories than to discriminate between pairs of stimuli drawn from between categories. This is a simple demonstration that these stimuli tend to constitute perceptual categories for both groups of birds.

The fact that isolate-reared budgerigars, hearing the sounds which make up the species repertoire for the very first time, show evidence of perceptual groupings for species-specific vocal signals has relevance for the problem of vocal learning. These results, and the fact that humans also tend to categorize these sounds in approximately the same way as budgerigars do (Dooling, Park, et al., 1987), suggest that these stimuli from different functional classes of calls within the budgerigar vocal repertoire are acoustically designed to be easy to categorize. In other words, vocalizations which budgerigars must ultimately learn, and which make up some of the major functional classes of vocal signals in the species vocal repertoire, form acoustically distinct categories. It is largely for this reason that budgerigars perceive these stimuli in roughly the correct manner the very first time they hear them.

But our results also show, by two different measures (i.e., MDS and cluster analysis of response latency matrices), that isolate-reared birds were subtly different from socially experienced birds in the way in which they perceive the relations among these categories of species-specific calls. The subjects weights from MDS show isolate birds separate from males and females with prior social experience with these calls and the dendrogram from a cluster analysis of the data from isolate-reared birds shows an intermixing of some call categories. These perceptual results parallel what we know from studying the vocalizations of this species. Budgerigars reared in acoustic isolation develop both abnormal songs (Farabaugh, Brown, & Dooling, Submitted) and calls (Dooling, Unpublished data) though not nearly as abnormal as those of birds deafened as young (Dooling, Gephart, et al., 1987). Together the results from these experiments provide a com-

pelling case for a role for perceptual learning in the ontogeny of the budgerigar vocal repertoire.

What do these results mean for the newly hatched budgerigar, faced with the challenge of developing a learned vocal repertoire? What does it have to cope with and what does it bring to the task? The two extremes are: (1) that nothing is specified perceptually, the bird's auditory world is a baffling, confusing assortment of acoustic stimulation, but through repeated exposure to the correct stimuli in the right context, the bird learns the appropriate perceptual categories for vocal signals, or (2) that perceptual categories for acoustic and functional categories of species-specific vocal signals are completely specified and perhaps even serve to guide the process of vocal learning. While the final answer to this question will have to await tests of very young animals, the present results from isolate-reared budgerigars are relevant to this issue since they show that, without the correct external auditory models and social situations, budgerigars fail to develop a completely veridical perception of the auditory world of complex vocal signals.

To be sure, the present results must be tempered by the fact that only two isolate-reared birds and only a selected sample of vocalizations from the species repertoire were used in these experiments. Nevertheless, these results are consistent with the notion that learning influences the auditory perceptual processes involved in vocal acquisition in this species. Elsewhere we have shown both socially-mediated perceptual learning of contact call categories in adult budgerigars (Brown, Dooling, & O'Grady, 1988) and evidence of specialized processing of these calls in adult birds (Dooling, Brown, Klump, & Okanoya, In Press). In aggregate, understanding vocal ontogeny in this species will require, in addition to auditory discrimination and categorical perception, knowledge of the important visual and social factors which serve to emphasize the biologically-relevant vocalizations for learning.

ACKNOWLEDGEMENTS

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THE PERCEPTION OF COMPLEX ACOUSTIC PATTERNS IN NOISE BY BLUE MONKEY (*CERCOPITHECUS MITIS*) AND HUMAN LISTENERS

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ABSTRACT: Blue monkeys (*Cercopithecus mitis*) were trained to detect complex acoustic signals embedded in noise. Masked thresholds were determined for four human consonant-vowel speech sounds (*ba, pa, ga,* and *ka*), and four blue monkey calls (*boom, pyow, chirp,* and *trill*). The ability of monkey listeners to hear these signals in noise was compared with humans. Results showed that monkey and human hearing was very similar. The mean difference between species for these eight stimuli in the broad-band noise environment was 2.3 dB. The signal-to-noise ratio for perception ranged from 4.8 dB for the *ka* to -23.8 dB for the *boom*. The four monkey calls were audible at a signal-to-noise level that was 8.1 dB less than that required for the detection of the speech sounds. However, most of this effect was due to the audibility of the *boom*. With the *boom* excluded, the mean signal-to-noise ratio for detection of the remaining 7 sounds was -0.5 dB, and the mean difference in the audibility of the speech and monkey sounds within this set was 2.6 dB. These results contrast with previous findings which used simulated rain forest noise as the masking noise (Brown, 1986). In rain forest noise, test signals were audible at signal-to-noise ratios approximately 10 dB less than those reported here, and the observed difference in the relative audibility of human and monkey utterances was larger. These findings suggest that rather small variations in the amplitude and spectrum of the ambient noise may have a strong influence on the audibility of vocal signals in nature.

INTRODUCTION

Many different species of animals are conspicuously vocal and they may signal acoustically over long distances in relatively noisy habitats (Moynihan, 1966; Payne & Webb, 1971; Morton, 1975; Gautier & Gautier, 1977; Byrne, 1981; Brenowitz, 1982; Brown & Schwagmeyer, 1984; Ryan & Brenowitz, 1985; Waser & Brown, 1986). The long-range calls of some forest primates, for example, may be audible for distances approaching 2 km (Brown, 1989a), and both the coordination of movement within a social unit, and the regulation of spac-

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ing between competing social units appear to be dependent upon the successful exploitation of the acoustic modality. Listeners are confronted with the task of distinguishing species-specific vocalizations from the calls of sympatric species. For example, in many instances forest monkeys may live sympatrically with perhaps a half dozen other species of primates, with scores of species of birds, and with hundreds of species of insects. Because rain forests exhibit a diversity of niches arrayed vertically as well as horizontally, this habitat exhibits a multitude of biotic sources of acoustic signals, and this rich assemblage of organisms in concert may generate a cacophony of background noise as each species struggles to make its own message heard (Waser & Brown, 1986; Brown & Waser, 1988).

Though the rain forest habitat may represent an end point for acoustic competition among vocalizers, the problem of hearing in noise is by no means restricted to rain forest inhabitants. In the tropical zone, the residents of the riverine forests and the savanna, and in the temperate zone the inhabitants of the grass lands, the swamps and the forests all encounter similar difficulties. Furthermore, in many instances the noise generated by other organisms is overshadowed by the noise produced by rustling vegetation, rain and thunder. Hence, in many niches an evolutionary premium may have been placed on the ability of organisms to detect and classify complex acoustic wave forms embedded in ongoing temporally fluctuating background noise (Brown & Waser, 1988).

Natural selection could act to heighten the audibility of vocal signals in noise by "improving" the acoustical structure of the signal so that it is more perceptible in noise, by "improving" the structure of the signal detection module of the auditory system so that it can "hear" signals at lower signal-to-noise ratios, or by simultaneously "improving" the design features of both the sound production and sound reception systems. It is clear that different species employ species-specific communication sounds that differ substantially in their audibility in noise. Blue monkeys (*Cercopithecus mitis*) and grey-cheeked mangabeys (*Cercocebus albigena*) have been shown to be able to hear their own species utterances at signal-to-noise levels that are about 10 dB below the level at which humans can hear speech sounds (Brown, 1986). Yet, the acoustical or perceptual reasons for these observed differences in the audibility of various signals is not fully known. Brown (1986) suggested that the vocalizations of rain forest monkeys evolved a structure that rendered them less susceptible to masking than human speech. However, it is unclear if calls produced by some primates have acquired a structure which in general is inherently more audible in any noise, or if selection has acted to "adjust" the acoustical features of various primate repertoires to cope specifically with the acoustics of the local habitat. Hence, in this con-

text, speech sounds may be found to be more audible than monkey calls if testing were conducted in an acoustic environment that corresponded to that in which speech sounds originally evolved.

In the present paper we explore this possibility by comparing the audibility of selected speech and monkey utterances in an acoustic environment which provides a spectral contrast to the rain forest habitat.

METHOD

Animals

Three adult male blue monkeys (*Cercopithecus mitis*) served as subjects. The monkeys were laboratory born, and ranged from five to six years in age. The primate laboratory animal care standards exceed both institutional and NIH guidelines. Experimental animals were weighed daily, and were maintained on a diet of Purina monkey chow supplemented with PRIMA-Treats and a diverse diet of fresh fruit and vegetables. Animals were fed twice daily, and maintained in a colony situation promoting social exchanges. Animals, individually housed, were supplied with foraging boxes, and had scheduled access to a "gymnasium" supplied with swings and other "toys." Attempts were made to breed selected animals. All monkey subjects were experimentally naive at the onset of training. Three human listeners (two males and one female) were also tested. The human subjects ranged in age from 21 to 28 years of age. All humans and monkeys were screened for hearing within normal limits for frequencies ranging from 125 Hz to 8,000 Hz.

Apparatus

Monkeys and humans were tested in a double-walled IAC model 1203 semi-anechoic room. The walls and ceiling of the room were covered with 10 cm thick Sonex acoustic foam. The absorption coefficient of this treatment was greater than 0.6 at 125 Hz and increased to 0.9 or more for frequencies above 400 Hz. The floor of the room was carpeted. Stimuli consisted of the human consonant-vowel speech sounds *ba*, *pa*, *ga*, and *ka*, and the blue monkey calls *pyow*, *boom*, *trill*, and *chirp*. This set of vocalizations samples the diverse range of calls in the blue monkey's repertoire (Marler, 1973). The *pyow* and *boom* calls are loud calls emitted exclusively by adult males. The *trill* and *chirp* calls are given by both juveniles and adult females. These vocalizations were selected because it is possible to obtain high-quality recordings of these signals in an acoustically controlled laboratory con-

text. All eight test stimuli were recorded in the laboratory. The speech sounds were recorded from a male talker with a Standard American dialect. The *pyow* and *boom* monkey calls were recorded from an adult male blue monkey, and the *trill* and *chirp* calls were recorded from an adult female blue monkey. The test signals were digitized on a 12-bit A/D converter at a sample rate of 27.5 kHz. Monkeys were seated in a Primate Products monkey chair during the course of the one hour daily session. Humans were seated in a conventional institutional chair in the same position in the sound field occupied by the monkeys. Auditory stimuli were presented free-field through a Polk 10 loudspeaker, and stimulus presentations were controlled by a Compaq 486/25 computer. The test stimuli were embedded in a broad band masking noise produced by a General Radio 1381 noise generator. The masking noise was presented at a level of 60 dBA.

Procedure

During 1 h daily sessions monkeys were trained with operant conditioning positive reinforcement procedures to contact a response key to initiate a trial and to terminate key contact upon detecting the presentation of an acoustic signal. The presentation of the acoustic stimuli was controlled by computer and occurred unpredictably according to a variable interval schedule (1-7 s). Following sound presentation, the termination of key contact within a 1.5 s response interval resulted in the delivery of a 190 mg banana-flavored whole diet food pellet (Bioserv). Terminating key contact at other times did not produce food reward, and started a 6 s time-out condition during which the experiment was suspended and the monkey was required to refrain from contacting the response disk.

The response key was illuminated from behind, and this light was off during either the time-out condition or during a 5 s intertrial interval which followed reinforcement, and which allowed adequate time for the monkeys to eat. To signal the availability of the next trial, the key light pulsed at a rate of 5 pulses per s, when the individual securely contacted the response key, the light became lit continuously. The test stimuli were embedded within a broad band noise background that came on at the onset of each trial. The masking noise was presented at a level of 60 dBA.

Masked auditory thresholds were determined by the computer through the staircase or tracking method. In this procedure, the SPL of the stimulus to be presented in the up-coming trial is governed by the individual's response to the previous trial. If the previous trial was detected, the SPL of the stimulus for the next trial was reduced; if the monkey failed to detect the preceding trial, the converse occurred. Hence, the method tracks the minimal SPL of the stimulus

required for the monkey to hear. Trained monkeys were initially presented with two different kinds of trials: test trails as described above (85%), and silent catch trials (15%) which permitted the measurement of the rate of guessing. A third type of trial presented clearly audible supraliminal stimuli; these trials always occurred immediately following the correct rejection of a catch trial, and they were programmed to ensure an adequate reinforcement density. Hence, the monkeys did not have to wait for very long intervals for the next detectable signal to be presented. This procedure has been found to produce a constant and uniform rate of responding.

Humans were tested with the same apparatus and with the same procedure as described above for the monkeys except that a wooden chair was substituted for the primate chair, and a click of the feeder served as feedback for a correct response, a food pellet was not delivered, and the intertrial intervals were reduced to 1 s in duration.

RESULTS

In Figure 1 we show the spectrum of the masking noise plotted in third octave bands. Though the acoustic source for the masker was white noise (equal energy per cycle), the acoustics of the room and speaker produced the resultant broad band spectrum. We compared this noise spectrum with the spectrum of rain forest, riverine forest and savanna habitats and found that the noise spectrum used here
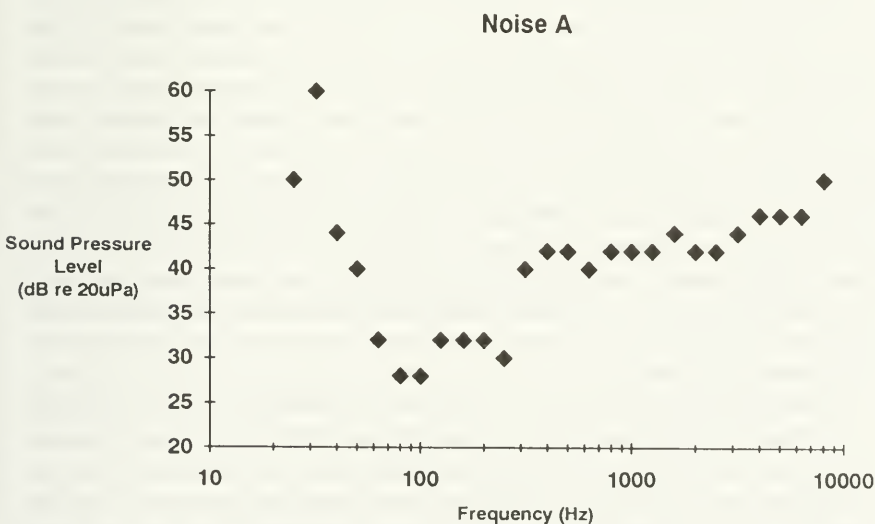
FIGURE 1. Spectrum in third-octave bands of the masking noise.
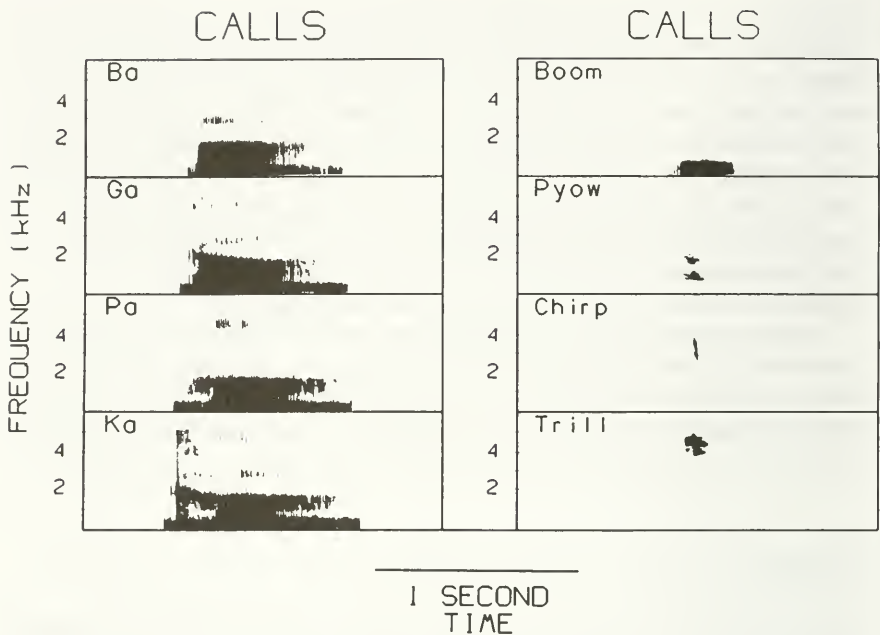
FIGURE 2. Sound spectrograms of the four human speech sounds (left panel) and the four blue monkey calls (right panel).

diverged strongly from those recorded in natural primate habitats (Waser & Brown, 1986).

Sound spectrograms of the eight test signals are presented in Figure 2. Signal duration ranged from 20 ms for the blue monkey *chirp*, to 880 ms for the *ka* speech utterance. The mean duration of the human speech sounds was 765 ms, while the mean duration for the monkey calls was only 115 ms. Hence, the human speech utterances were on the average 6.7 times longer than the blue monkey vocalizations. The sound spectrograms also reveal that the monkey vocalizations exhibited substantial diversity in dominant frequency. The *boom* call's dominant frequency was centered at 160 Hz, while the *chirp* and *trill* call were centered near 4 kHz. The dominant frequency band (Fo) of all four of the human speech sounds was centered near 1 kHz, and the speech sounds were much broader in bandwidth than the monkey vocalizations.

In Figure 3 we show the relative audibility of the test signals embedded in the broad band masking noise. The data shown here are averaged for six sessions. The performance of all listeners was very stable across sessions. The data for the humans are given by the open bars, and the data for the monkeys are displayed by the solid bars. There was very small variability among the listeners, the standard
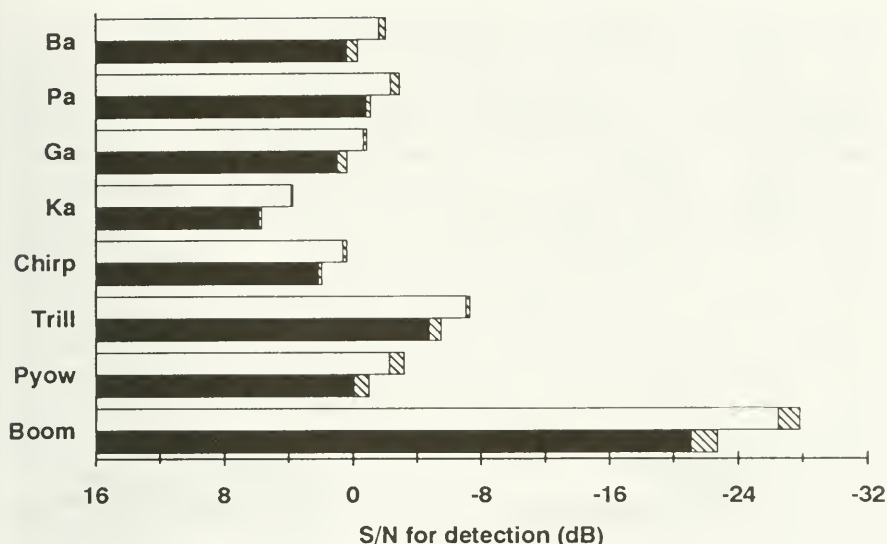
FIGURE 3. Signal-to-noise ratios for the eight test signals for human listeners (open bars) and monkey listeners (solid bars). Three individuals were in each group, and the standard error of the mean is denoted by the striped area at the end of each bar.

error of the mean was very small, and this is displayed by the striped area at the end of each bar.

The signal-to-noise ratio for detection ranged from 5.8 dB for blue monkeys presented with the *ka* sound to −26.5 dB for humans presented with the *boom* call. The results show that blue monkeys could detect these signals in noise nearly as well as human listeners. Humans were able to hear these signals on the average at a level that was 2.3 dB less than that heard by blue monkeys. The mean audibility of the speech sounds by humans was −0.25 dB, while the blue monkeys detected the same signals at a mean level of 1.53 dB. This yields a difference in sensitivity between humans and monkeys of 1.78 dB for the human speech sounds. The mean audibility of the monkey calls by humans was −8.85 dB, and the corresponding value for blue monkeys was −5.97 dB. This results in a difference in sensitivity between humans and blue monkeys of 2.88 dB for the blue monkey utterances. These findings are in keeping with other studies that show that humans are just a little bit more sensitive than nonhuman primates in most psychoacoustical tasks (Stebbins, 1973).

Pooling the data across species, the four monkey calls were audible at a mean signal-to-noise level that was 8.1 dB less than that required to hear the speech sounds. However, as is readily notable from inspection of Figure 3, most of this effect is due to the superior
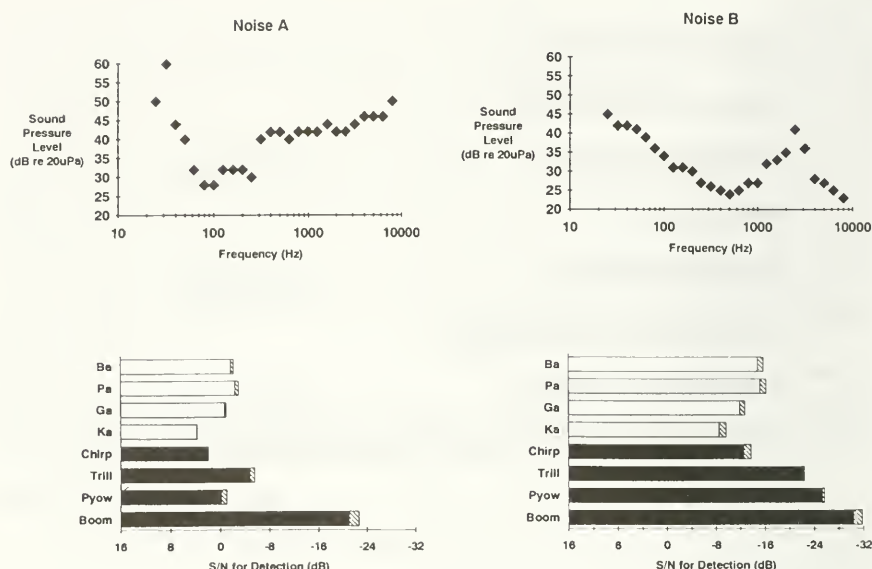
FIGURE 4. Signal-to-noise ratios for two noise spectra. The noise spectra are presented in the top panel. Noise A is the noise spectra presented here, Noise B is simulated rain forest masking noise (Brown, 1986). The corresponding signal-to-noise ratios for the eight test stimuli are given in the lower panel. Data are presented for conspecific listeners only.

audibility of the blue monkey *boom* vocalization. With the *boom* excluded from analysis, the mean difference in the audibility of the speech and monkey sounds was 2.6 dB. Hence, in the presence of the broadband masker used here, the blue monkey calls in general were slightly more detectable in noise than were the speech sounds, but this effect was not very strong.

DISCUSSION

These observations contrast with previous findings from our laboratory which used simulated rain forest noise as the masking sound (Brown, 1986). In Figure 4, top panel, we present spectra of the broadband masking noise used here, and the simulated rain forest masking noise used in earlier work. In the bottom panel of Figure 4 we show the relative audibility in noise of the 8 test stimuli detected by conspecific listeners in the two noise environments. Because Brown (1986) only tested the monkey calls with monkeys and the speech sounds with the humans, we plot the corresponding data in Figure 4.

Two observations are important here. First, the test signals were in general more audible when testing was conducted with the rain forest masker. Averaged across calls, the signal-to-noise ratio for the detection of this set of stimuli was -17.6 dB when testing was conducted with the rain forest masker, and -3.4 dB when testing was conducted with the broadband masker. Thus, the shape of the noise spectrum appears to have a strong effect on the relative audibility of complex signals in noise. Second, when testing was conducted with the rain forest masker, the monkey calls were audible at a relative level that was 10 dB less than that required for the detection of speech sounds (Miller, 1947; Hawkins & Stevens, 1950). As noted above, this effect was amplified by the superior audibility of the *boom* call. However, even after the *boom* was excluded from analysis, the monkey calls were still 7.4 dB more audible than the speech signals. This contrasts with the 2.6 dB value obtained above with the broadband masker. Thus, though the blue monkey calls examined here have a physical structure that enhances their audibility in noise relative to that for speech sounds, the results suggest that rather small variations in the spectral or amplitude characteristics of the noise present in the acoustic environment may have a strong influence in the audibility of vocal signals in nature.

Brown (1986) argued that forest monkeys had undergone selection to produce vocalizations that were more audible in noisy environments than were human speech sounds. However, it is unclear if the 10 dB difference reported by Brown (1986) was due to differences in the acoustics of monkey calls and human speech, the characteristics of the masking noise used, or differences in the abilities of humans and monkeys to detect complex sounds embedded in noise. The results of the present study show that blue monkeys are not in general better than human listeners in detecting complex signals in noise. Humans detected both monkey sounds and speech sounds at slightly lower signal-to-noise ratios than did the monkeys. It appears likely that humans would have performed similarly to monkeys in the rain forest masking noise (Noise B) if both species had been tested on both sets of stimuli. In contrast, the results suggest that differences in the audibility of speech and monkey sounds in the ecologically valid rain forest masking noise was due to both the spectral characteristics of the masking noise and species-specific differences in the structure of human and blue monkey vocal signals. Interestingly, the very brief blue monkey calls are more audible in noise for both human and monkey listeners than is the much longer duration human speech stimulus, and this effect is amplified when testing is conducted in noise that mimics the spectral characteristics of the natural environment.

As a rule, researchers in psychoacoustics have given little attention to the spectral and temporal characteristics of masking sounds

used in perceptual studies (Brown, 1986; 1989a). Though researchers study the perception of biologically significant signals (e.g., vocalizations), they typically employ masking noises in these and in related studies which have no ecological validity or biological significance. Most researchers appear to tacitly assume that all masking sounds are approximately equivalent impediments to hearing. However, each natural habitat exhibits a constellation of acoustical characteristic that are likely unique unto itself (Brown & Waser, 1984; 1988; Waser & Brown 1986; Brown, 1989a; 1989b), and because communication systems evolved within a specific acoustical environment it is probable that the structure of some systems underwent selection to counter the impediments to acoustic communication characteristic of the local habitat. The observation that blue monkey calls are audible at lower signal-to-noise ratios when embedded in the rain forest masker compared to when embedded in a broad band masking noise that lacks ecological validity or biological significance is consistent with this hypothesis. The idea of a match between the acoustic structure of the vocal repertoire and habitat acoustics should be explored more fully by testing the audibility of species-specific vocal signals in primates resident in riverine and savanna habitats with ecologically appropriate and inappropriate masking noise.

How can it be that two different masking sounds with different spectral characteristics change the audibility of signals in noise? To our knowledge there has been no systematic study of the influence of various maskers on the audibility of signals in noise. However, several possible mechanisms merit comment. First, it is possible that the spectral density may be lower near the dominant frequency band of any test signal in one masking sound relative to that for another. For example, in Figure 4 the spectral density of Noise A is lowest at 80 Hz and 100Hz, while the spectral density of Noise B is lowest at 630Hz. These differences in the shape of the noise spectrum may account for the global differences in the audibility of the test signals embedded in the two noise samples. Many of the test signals have a dominant energy band near 1000 Hz, a region of low spectral density in Noise B, and it is possible that these signals are more audible in Noise B because they fall in a quiet zone within the spectrum of the noise. However, this explanation cannot account for the enhanced audibility of the *boom, chirp*, and *trill* vocalizations in Noise B. In these three cases, the spectral density of Noise B is approximately the same as that in Noise A at the dominant frequency region of the sound.

This observation suggests that differences in the audibility of various signals in different noise environments may not simply be due to a fortuitous congruence between "quiet zones" in the masker and the dominant frequency band of the signal. Brown (1989b) has suggested that the auditory system of many organisms may have been "designed" to promote the detection of signals in noise. Both

psychoacoustical and physiological observations are pertinent to this hypothesis. For example, Young and Barta (1986) noted that the rate-intensity function of single units recorded in the cat were steeper if the test signals were presented in noise than if they were presented in the quiet. It was as if the auditory system functioned with greater precision under the biologically normal conditions of the presence of a background noise. Preliminary behavioral observations from our laboratory also reveal certain conditions in which the presence of noise improves perception. We have observed, contrary to our initial expectations, that monkeys reveal smaller frequency difference limens when tested at low sensation levels compared to larger sensation levels, or if tested at higher sensation levels when a masking sound is present. It is as if the monkey's auditory system "expects" the presence of masking noise, and it is "designed" to function best in the noise context.

These observations are consistent with the idea that the communication systems of some organisms have been selected to promote hearing in noise, and that the acoustical attributes of ecologically appropriate background noise may "interface" with the signal detection module of the auditory system in unexpected ways. In this perspective, it is as if each place in the natural world has its own special ambient sound, and that the ears of the organisms resident in each acoustic environment have undergone selection to be able to quickly discern the occurrence of a sound that does not belong, a sound which may signal the approach of a competitor, a predator, a relative, a mate, or one's prey. Classically the auditory system has been studied with biologically and ecologically irrelevant stimuli, pure tones, tone pips, clicks, noise bands, and the like. Though many investigators now study the auditory processing of species-specific communication sounds, few investigators are studying the perception of these signals in an ecologically "appropriate" acoustic environment. The data presented here suggest that a full understanding of the organization and design of the auditory system will require researchers to examine perceptual processes within the acoustic environment in which communication normally occurs and in which it evolved.

ACKNOWLEDGEMENTS

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HUMAN INFANTS' PERCEPTION OF AUDITORY PATTERNS

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ABSTRACT: Human infants' perception of tone sequences or melodies is reviewed in the context of related work with human adults and nonhuman species. For the most part, infants use an adult-like pitch processing strategy that is global and relational rather than the local pitch strategy that is characteristic of the nonhuman species studied to date. Thus they encode and retain the pitch configuration or contour of a melody, with little attention to the absolute pitches of individual notes. In the case of well structured melodies, specifically, melodies that are prototypical of Western music, infants encode more precise relations, notably the intervals or exact pitch relations between adjacent notes. Finally, the functional significance of relational pitch processing in human infancy is considered.

The study of immature listeners provides opportunities for exploring the role of experience in mature listeners' perception of complex patterns. To the extent that experience plays an important role, this would increase the likelihood of cross-species parallels in early life and of cross-species differences later on. In fact, current research on the perception of complex auditory (nonspeech) patterns by human adults emphasizes the plasticity of pattern perception processes and the dependence of perceptual organizational processes on extended experience and expectations (Espinoza-Varas & Watson, 1989). It is possible, then, that the pattern processing strategies of human infants, by virtue of limited experience and the absence of language, might differ substantially from those of adults, bearing greater similarity to those of some nonhuman species.

To date, the human-nonhuman comparisons of auditory pattern perception have focused primarily on speech, specifically, single speech sounds (Kuhl, 1989). The goal of such comparisons is to determine whether phenomena that are critical to speech perception such as categorical perception (Liberman, Harris, Hoffman, & Griffith, 1957) and auditory equivalence classification (Kuhl, 1979; 1983) involve speech-specific (i.e., species-specific) mechanisms or more general auditory mechanisms that are shared by other species (for re-

views see Dooling, Brown, Park, & Okanoya, 1990; Kuhl, 1987; Moody, Stebbins, & May, 1990). In our own research, we have departed from this approach, choosing to examine human infants' processing of serial pitch patterns, notably tunes or melodies (for reviews see Trehub, 1985, 1987, 1990; Trehub & Trainor, 1990, in press). This may seem like a highly specialized endeavor with limited application but music is found in every human culture, just as language is. All of us participate in music, as listeners if not performers, but the biological significance of music remains a mystery (Granit, 1977; Lerdahl & Jackendoff, 1983). Nevertheless, human music processing capacities have captured the attention of comparative researchers, leading to studies of tune discrimination in rats, songbirds, and monkeys (for reviews see D'Amato, 1988; Hulse & Page, 1988; Hulse, Page, & Braaten, 1990). This enables us to use the human adult findings as one anchor and the nonhuman findings as another in our research with human infants. For example, relational processing in the pitch domain (i.e., relative pitch) typifies human adults' processing of tunes but not that of the nonhuman species studied to date. Instead, those species that can discriminate contrasting tunes do so primarily by remembering the exact pitch levels of one or more tones (D'Amato, 1988). Indeed, Premack (1983) has commented on the human predilection for relational responding to complex stimuli and the nonhuman predilection to do otherwise. What about human infants?

To study infants' perception of tunes or melodies, we present 7- to 11-month-olds with a sequence of five or six pure tones and then test for their detection of deviations from that sequence (for methodological details see Trehub, Bull, & Thorpe, 1984; Trehub, Thorpe, & Morrongiello, 1987). We can vary the difficulty of the task by manipulating the length and complexity of the sequences, the size of the retention interval, and/or the degree of deviation from the original sequence. In this way, we can obtain information about aspects of the pattern that are salient and memorable for infant listeners.

Specifically, we present a repeating melody (i.e., the standard or background pattern) from a loudspeaker to one side of the infant (left), and periodically substitute a melody (i.e., the comparison pattern) that is altered in some respect. The background melody is presented repeatedly from the moment the infant enters the test environment (a sound-attenuating booth) until the completion of the test session. The tester and attending parent wear headphones with masking patterns so that they remain unaware of the specific stimuli being presented to the infant at any time. The tester indicates to a computer (via a button-press) when the infant is attentive and looking directly ahead; test trials are only presented at such times. She also indicates (via another button) when the infant turns at least 45° to the loudspeaker. The computer monitors such turns, on the one

hand, and the occurrence of melody changes (i.e., the comparison pattern), on the other. Whenever the computer records a response (45° head turn) within 4 s of a melody change, it delivers reinforcement in the form of illumination and activation of one of four (randomly selected) mechanical toys in a darkened Plexiglas box near the loudspeaker. In effect, this is a GO/NO-GO procedure, with the standard stimulus functioning as S − and the comparison stimulus as S +. Trials are not signalled in any way so that S − trials are essentially indistinguishable from the background repetitions. This is rather different from the typical implementation of GO/NO-GO procedures with nonhuman or human adult listeners.

To ensure that infants understand the task demands, we require them to meet a training criterion of four successive correct responses to a salient (i.e., clearly discriminable) change within a maximum of 20 trials. Most infants initially orient to the sound change and, therefore, train relatively quickly. During the subsequent test phase, we present approximately 30 test trials (more trials in some experiments, less in others), half of which incorporate some change in the melody (more subtle than that presented in the training phase), the other half involving no change, with the change and no-change trials presented in random order. Some spontaneous turning toward the toys can be expected so that the no-change or control trials are essential for unequivocal interpretation of performance on the change trials. If infants turn significantly more on the change than on the no-change trials, this indicates that they can detect the change in question.

ADULT MELODY PERCEPTION

Some facts about adult melody perception provide a context for evaluating infant performance in this domain. Adults' recognition of melodies does not depend on specific notes or exact pitch levels but rather on the *relations* among component notes. The key to tune recognition, in the case of *familiar melodies* (i.e., those with extended exposure in everyday life, or highly overlearned melodies that can be recalled or recognized), is the pattern of *intervals* (Attneave & Olson, 1971; Dowling & Fujitani, 1971), with intervals referring to the precise relations between adjacent notes (fundamental frequency ratios or distance in semitones between successive notes). Thus we perceive transpositions, which have different notes but an identical pattern of intervals, as equivalent to the original and, in many circumstances, indistinguishable from it (Attneave & Olson, 1971). With *unfamiliar melodies* (i.e., those introduced in the test situation), tune recognition depends on configurational information about pitch (Bartlett & Dowl-

ing, 1980) or the pattern of successive directional changes (ups and downs) in pitch, which is known as *melodic contour* (Dowling, 1978). Contour refers only to directional aspects of the pitch changes (whether they rise, fall, or stay the same), not their extent (Dowling & Harwood, 1986). Finally, melodies that conform to the musical structure of our culture are processed in greater detail, learned and remembered more readily, and are preferred over melodies that violate such structure (Cuddy, Cohen, & Mewhort, 1981; Krumhansl, Bharucha, & Kessler, 1982; Krumhansl & Keil, 1982; Lynch, Eilers, Oller, Urbano, & Wilson, in press).

MELODY PERCEPTION: NONHUMAN COMPARISONS

Many nonhuman species have elaborate vocal communication systems, raising the possibility of specialized systems for processing complex auditory patterns (Beecher, Petersen, Zoloth, Moody, & Stebbins, 1979; Hulse et al., 1990; Nelson & Marler, 1990). Nevertheless, research on tune discrimination in various nonhuman species has revealed a pattern of skills and strategies that is very different from that of human adults. In these studies, the animals in question are typically trained to respond (e.g., key peck, lever press) to S+ and to withhold responding to S−, with S+ and S− being presented on distinct and clearly signalled trials. The animals are subsequently tested on their generalization of the trained response to novel exemplars.

Although initial studies with albino rats and cebus monkeys seemed to indicate that these species, after extensive training, were capable of melody discrimination (D'Amato & Salmon, 1982), such discriminations were later found to be based primarily on local (i.e., individual, absolute) pitch cues rather than global pattern cues such as contour (D'Amato, 1988; D'Amato & Salmon, 1984). When cues such as common pitches or pitch range between training and generalization stimuli were removed, the animals tended to perform at chance levels, even after thousands of training trials. Similar difficulty with pitch contour discrimination has been observed in starlings (Cynx, Hulse, & Polyzois, 1986; Hulse & Cynx, 1985, 1986) and budgerigars (Dooling, Brown, Park, Okanoya, & Soli, 1987), although there are disputed claims for rudimentary contour perception when the preferred strategy (absolute pitch) is blocked (Hulse & Cynx, 1986; Hulse et al., 1990; but see D'Amato, 1988). These findings cannot be attributed to the arbitrary nature of the tunes because, in some cases, the stimulus tunes were modeled on species-typical calls (e.g., Dooling et al., 1987).

An absolute pitch strategy can be seen as highly appropriate for

avian, if not for human, listeners. Although there is insufficient documentation of the acoustic cues for individual and species recognition in most bird species, the available research seems to indicate that absolute pitch is the principal cue (Brooks & Falls, 1975; Nelson & Marler, 1990). Brooks and Falls' (1975) research on the white-throated sparrow is especially informative in this regard. In the songs of the white-throated sparrow, pitch is relatively constant for each individual and varies over a narrow range within the species. By contrast, there is little consistency in the number or duration of notes in a song. In fact, the absolute pitch of the first one or two notes seems to be critical in the identification of individual, white-throated sparrows and of conspecific neighbors. This focus on absolute as opposed to relative pitch in sparrows, budgerigars, and many other species is not attributable to inadequate resolution of the relative pitch differences but rather to the greater salience of absolute cues in the sound environment of these species (Brooks & Falls, 1975; Dooling et al., 1987; Nelson & Marler, 1990).

INFANT MELODY PERCEPTION: CONTOUR PROCESSING

If human infants were exposed to a melody in the context of the conditioned head turn procedure described previously, what would they encode and remember? There are several possibilities. They might recognize all of the notes of a very brief melody and, perhaps, the first or last few notes of a longer melody. This would involve a local or absolute pitch strategy, one that is congenial to songbirds (Brooks & Falls, 1975; Dooling et al., 1987; Hulse & Cynx, 1986; Hulse, Cynx, & Humpal, 1984), rats, and monkeys (D'Amato & Salmon, 1984). Alternatively, they might encode the melody relationally, attending to a global property such as its pitch contour (adults' strategy with unfamiliar melodies) or to a more precise property such as its pattern of intervals (adults' strategy with familiar or highly overlearned melodies). The interval strategy would seem to be unlikely for a number of reasons. Adult-like processing of specifically musical as opposed to general auditory information is thought to require extended exposure to the music of one's culture (Jones, 1982; Krumhansl, 1990). Moreover, no tunes could possibly have the status of familiar or highly overlearned melodies in infancy. Nevertheless, it should be possible to gain information about melodic processing strategies in infancy from the kinds of melodic changes that infants can detect together with those that they cannot detect.

In one study (Trehub et al., 1984), we tested infants for their discrimination of various changes to a six-note melody (i.e., a sequence of six pure tones), including *transpositions* (different notes,

same intervals and contour), *contour-preserving* changes (different notes and intervals, same contour), and *contour-violating* changes (same notes in different order, resulting in different intervals and contour). With the exception of the transpositions, all contrasting melodies began and ended on the same note as the standard melody, thereby precluding the use of single-note cues. From the perspective of human adults, the transposed tunes would be most similar to the original melody by virtue of identical pitch relations; those with altered contour would be least similar by virtue of altered pitch relations. From the perspective of songbirds, rats, or monkeys, however, the patterns with altered contour (identical first and last notes, internal notes permuted) might be most similar to the original melody on the basis of absolute pitch cues. Moreover, the transpositions, which embodied more absolute pitch changes than the other comparisons, would be least similar for nonhuman listeners.

In one condition (Experiment 1), the standard and test melodies were separated by 800 ms (brief retention interval); in another (Experiment 2), they were separated by 2.6 s (longer retention interval) and the interpattern interval was filled with repeating notes. When the retention interval was brief, infants detected all of the changes, performing best, however, on the contour changes. With longer retention intervals, they readily detected the contour changes (identical but permuted notes) but failed to respond to the transpositions (all new notes) or to the contour-preserving changes (some new notes). It appeared, then, that precise pitch and interval information decayed rapidly, leaving global information about contour intact. In fact, infants were subsequently shown to detect subtle contour changes generated by a single-note change within a six-note melody (Trehub, Thorpe, & Morrongiello, 1985).

In a further study (Trehub et al., 1987), we presented infants with an even more challenging task. They had already shown us that they could discriminate contour changes in the context of a fixed repeating melody or single standard. Now we asked them to discriminate contour changes in the context of five-note melodies that varied from one repetition to the next (Figure 1). The repeating melodies of one set had different component notes or pitches but a common contour (up-down). The contrasting set had melodies with the same component pitches as the standard set but reordered so as to generate a different contour (down-up-down). The infant's task was to ignore the local pitch changes within each set of patterns and to respond on the basis of the contrasting contour between sets. Infants were successful on this task, indicating that they could discriminate sets of melodies on the basis of contour alone and, moreover, that they could recognize similarities among discriminable melodies with common contour. In other words, they demonstrated auditory equivalence classification or
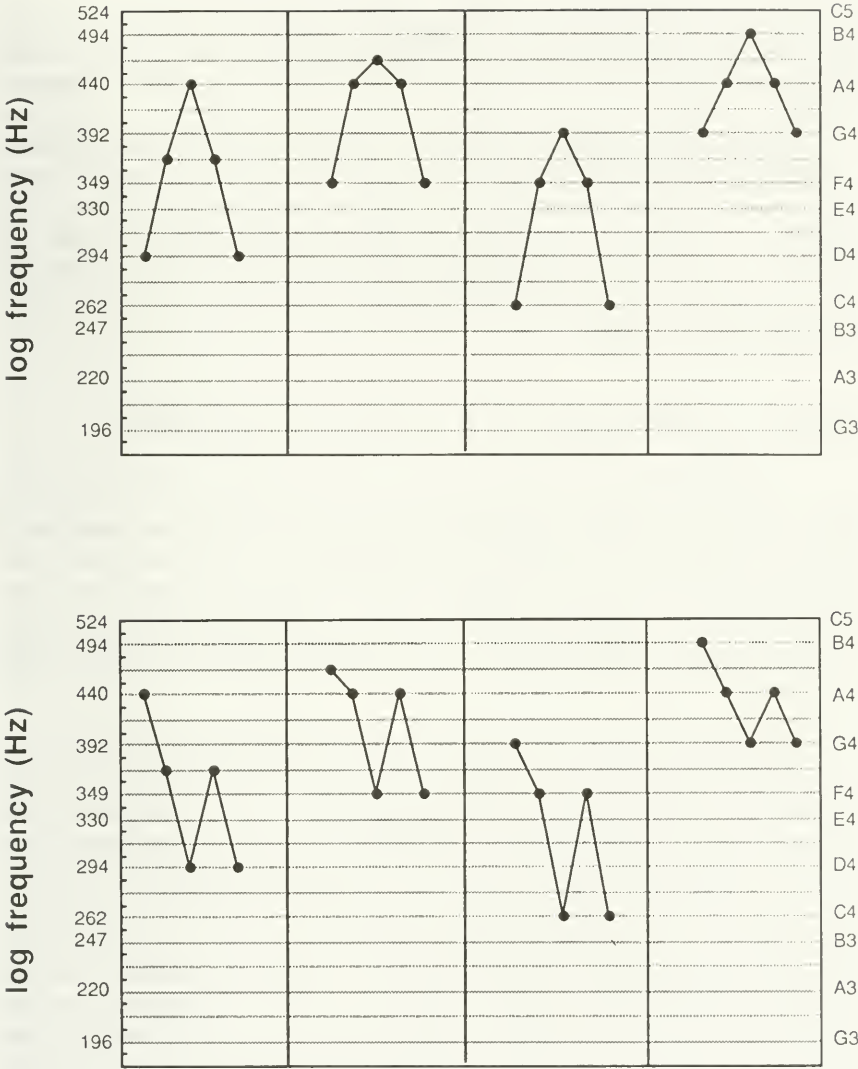
FIGURE 1. Sample melodies from Trehub et al. (1987). Upper panel: set of contour-preserving (variable interval) melodies. Lower panel: contrasting set with changed contour. Successive horizontal lines represent note names and associated numbers denote the relevant octave.

perceptual constancy for melodic contour. Of further interest is the fact that performance was unrelated to the age of infants (7-11 months) in this or any of our other investigations of melody perception.

These studies, taken together, reveal that infants' perceptual processing of melodies (unfamiliar ones, of course) has much in common with adults' processing of unfamiliar melodies, with contour playing a critical role in both cases. Moreover, infants' relational approach to melody perception has relatively little in common with the local or absolute pitch strategy that predominates in the nonhuman species studied to date.

INFANT MELODY PERCEPTION: INTERVAL PROCESSING

Although it is generally the case that infants extract the contour and not the intervals of melodies, especially when the task is difficult (long retention intervals or variable melodies), there are some notable exceptions. In recent studies, we have shown that when the standard melody is a prototype or highly typical example of Western musical structure, infants seem to be capable of encoding intervallic relations, detecting changes as small as a semitone in a single note of a melody.

Some background information about Western tonal music may be necessary for clarifying this issue. Each octave (pitch ratio of 2:1) is divided into 12 equal intervals (semitones) that form the *chromatic* scale. Western tonal music is not based on this equal-interval chromatic scale but on the unequal-interval *diatonic* scale, which consists of seven notes from the chromatic scale. Designating the key or reference note of a melody implies an appropriate set of notes, specifically the seven notes of the relevant diatonic scale and those having the same position (or note name) in other octaves. Moreover, various notes and note sets within the diatonic scale are considered to have special structural and functional significance. For example, the *major triad* (consisting of the 1st, 5th and 7th position of the chromatic scale or 1st, 3rd and 5th position of the diatonic scale) is structurally central to Western music theory (Schenker, 1906/1954) and has unique mathematical properties (Balzano, 1982). Moreover, it occurs frequently in Western music (Roberts & Shaw, 1984; Simonton, 1984), has a stable mental representation (Krumhansl et al., 1982), and is considered a prototype of diatonic structure (Cuddy & Badertscher, 1987). Prototypical melodies, which are presumably internalized on the basis of extended exposure to the music of a culture, provide a perceptual frame of reference against which to evaluate current melodic input (Jones, 1981).

We explored infants' ability to detect a semitone change in the context of a simple, well-structured melody based on the major triad (Cohen, Thorpe, & Trehub, 1987). The standard or background set of melodies consisted of C E G E C and its transpositions; the comparison set consisted of C E G$^{\#}$ E C and its transpositions. Thus the standard and comparison melodies involved a set of exemplars or variable repetitions (Cohen et al., 1987; Trehub et al., 1987) as opposed to a single exemplar of each (Trehub et al., 1984, 1985). Instead of the salient contour cues of the previous studies (Trehub et al., 1984; 1987), the comparison melodies in this study offered subtle interval cues, cues that infants tended to ignore. In this case, however, infants succeeded in detecting the change. In another condition, the background set of melodies was less well structured (C E G$^{\#}$ E C and its transpositions) in the sense that one note (G$^{\#}$) was incorrect or outside the appropriate key (C major in this case); the comparison set consisted of C E G E C and its transpositions. Thus, infants now had to respond to a *good* comparison melody in the context of a *bad* standard; previously they had responded to the same *bad* melody in the context of the same *good* melody as standard. Infants failed to detect these changes, implying that subtle interval changes were apparent only when a *good* standard melody was available as a stable frame of reference.

This surprising finding of enhanced infant performance in the context of well-structured patterns is in line with enhanced adult performance for *good* melodic (Bharucha, 1984) and rhythmic (Bharucha & Pryor, 1986) materials. The implication is not that infants are absolutely unable to discriminate subtle changes to so-called *bad* melodies or to melodies that do not conform to cultural conventions. On the contrary, infants may be able to discriminate such changes when other task demands are minimized. For example, infants were able to detect a semitone change to the less well-structured melody when the background repetitions were identical rather than variable (Trehub, Cohen, Thorpe, & Morrongiello, 1986). In comparable situations with identical repetitions, Western infants have also demonstrated their ability to detect subtle changes to melodies based on a foreign (Javanese pelog) musical scale (Lynch, Eilers, Oller, & Urbano, 1990). In the latter case, it is unclear whether their performance was based on the *goodness* or integrity of the foreign pattern or on the minimal task demands (i.e., identical repetitions). In any case, the combination of a poorly structured pattern and difficult task is sufficient to degrade the discrimination performance of infant listeners.

In a further study (Trehub, Thorpe, & Trainor, 1990), we explored the generality of the finding of interval processing in the context of *good* melodies. The five-note melodies in Cohen et al. (1987) had been simple, symmetric, and limited to three different notes.
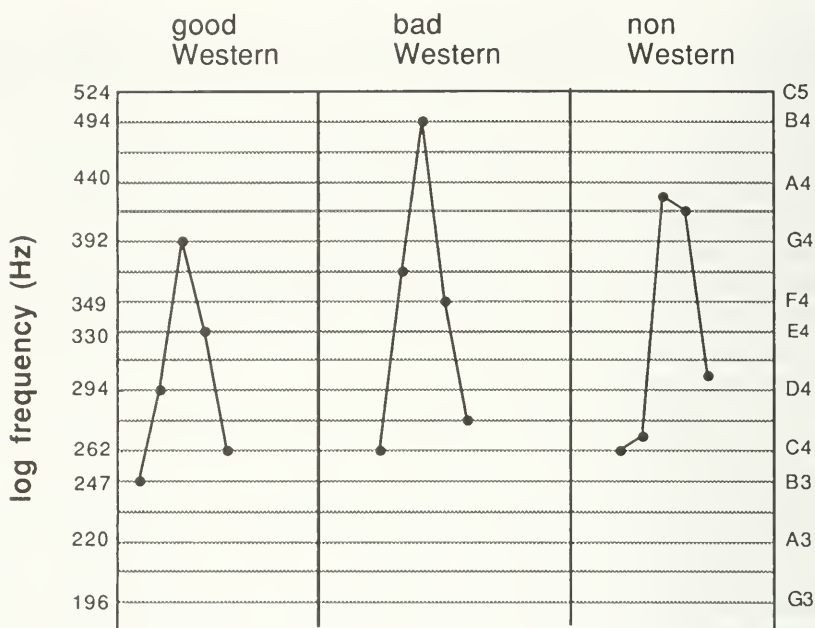
FIGURE 2. The *good* Western melody, *bad* Western melody, and non-Western melody from Trehub et al. (1990). Successive horizontal lines represent note names and associated numbers denote the relevant octave.

Would infants also exhibit differential processing of more complex melodies on the basis of their internal pitch structure? We generated three patterns with similar (rise-fall) contour and pitch range (Figure 2). The first melody (B_3 D_4 G_4 E_4 C_4 and its transpositions) was based on the major triad (the notes C E G) and could be considered *good* from the perspective of Western music theory (Piston, 1969; Schenker, 1906/1954) and psychoacoustics (i.e., simple integer ratios of adjacent notes, see Terhardt, 1978; Watkins, 1985). The second melody (C_4 $F^{\#}_4$ B_4 F_4 $C^{\#}_4$ and its transpositions) could be considered *bad* from a Western musical perspective in that its notes were drawn from the chromatic scale but not from any diatonic scale. Moreover, it contained two intervals that are considered to be highly dissonant (C_4 to $F^{\#}_4$; B_4 to F_4). The third melody could be considered *bad* as well as non-Western because its notes were not drawn from the chromatic scale. In fact, two of its intervals were smaller than a semitone but were still well within the frequency-resolving capability of infants (Olsho, Schoon, Sakai, Turpin, & Sperduto, 1982).

The infant's task was to detect a semitone change in the fourth position of each five-note melody. Since the three melodies had the same contour (up-down), note set size ($N = 5$), and timing (equal
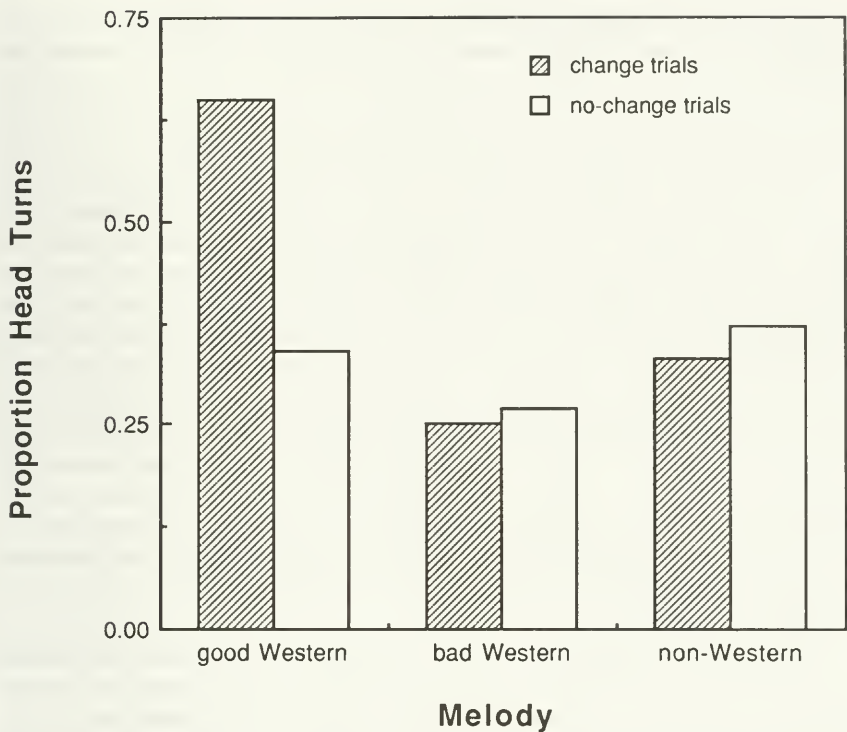
FIGURE 3. Average proportion of head turns on change trials and no-change (control) trials for each melody.

spacing between notes), any differences in performance would be due to differences in the melodic or pitch structure of such melodies. If diatonic structure is salient for infant listeners by virtue of pattern processing predispositions or experiential factors, then there should be facilitation for the *good* melody. If chromatic or semitone structure is relevant to infant perception, then infants should perform better on the two Western melodies than on the non-Western melody. In fact, infants responded to the semitone change only in the context of the *good* Western melody (Figure 3), suggesting that diatonic structure in general or major triadic structure in particular embodies some performance-enhancing properties, as yet undefined. There are further implications of these findings of interval processing in the context of prototypical or diatonic melodies. Specifically, the findings raise questions about adults' interval-processing strategy in the case of so-called *familiar* melodies. Is the interval-processing strategy engaged by the familiarity of the melody, as presumed, or is it engaged by special structural features of the melody? In most research on melody perception, *familiar* melodic structures and *good* melodic structures

have been confounded. In fact, it is difficult to unconfound them unless *good* (i.e., prototypical) patterns from foreign cultures are used as stimuli.

ADULT-INFANT DIFFERENCES: EXPERIENTIAL EFFECTS

The picture that seems to be emerging is that, like their adult counterparts, human infants exhibit enhanced processing for *good* auditory patterns, although the defining features of *good* patterns remain to be determined. Although perceptual predispositions, and perhaps exposure, play a role in the converging strategies of infants and adults, it is likely that musical acculturation would generate some strategic changes in auditory pattern processing. For example, our musical culture defines not only the *goodness* or acceptability of a sequence of notes but also the acceptability of various changes to that sequence. Given a *good* melodic context, subsequent changes could preserve its inherent structure or violate that structure. Presumably, structure-violating changes would be jarring, at least for experienced listeners, and, therefore, should be more noticeable than structure-conserving changes.

Recently, we examined the ability of 8- to 9-month-olds and adults to detect changes to a *good* or well-structured melody (Trainor & Trehub, in press). The standard or background melody was a sequence of 10 notes that embodied typical elements of Western melodic structure. In one condition, a note was changed by four semitones such that the resulting pattern was optimally consistent with the original melodic structure (diatonic change). In another, the note was changed by one semitone only but the change violated the structural conventions of Western music (nondiatonic change). The standard and comparison melodies were presented in transposition so that the discrimination could be accomplished only on the basis of relative as opposed to absolute pitch cues. Would listeners respond to the larger pitch difference, ignoring the musical structure, or would they respond to the structural change, ignoring the degree of pitch difference? One would expect musically naive listeners such as infants to find the diatonic change more salient (i.e., greater pitch difference but similar structure) and experienced listeners to find the nondiatonic change more salient (i.e., structural discrepancy but smaller pitch difference).

In fact, adults with no formal music training but the usual incidental experience readily detected the smaller nondiatonic change but failed to detect the larger diatonic change. By contrast, infants detected both changes equally well. Thus, although infants detected the change in relative pitch (i.e., interval change) from standard to comparison melody, the size of the pitch change was irrelevant to

their performance. What is particularly notable, however, is that the level of infant performance on the diatonic change was significantly better than that of adults. This does not reflect special skill on the part of infants but rather special difficulty on the part of adults. Indeed, adults' difficulty detecting the diatonic change in the context of a task designed for infants, a task involving numerous repetitions of the standard melody, underlines the profound processing changes that arise from musical acculturation.

In short, the suggestion that emerges from these findings is that musical acculturation builds on relational processing predispositions that are evident in early life, leading to the perceptual enhancement of culturally relevant information about musical structure at the expense of culturally neutral information about pitch distance. Furthermore, infants' ability to discriminate melodic changes that are not apparent to adult listeners parallels their facility with some foreign language discriminations that pose difficulties for adults (Trehub, 1976; Werker & Lalonde, 1988; Werker & Tees, 1984). In other words, acculturation may involve some refocusing of attention such that certain acoustic differences that are distinguishable but do not signal meaningful consequences (e.g., *l* and *r* for Japanese speakers) may be ignored by experienced listeners in favor of other distinctions that signal more meaningful consequences.

One challenge for future research is to specify the features that define *good* melodies for infant listeners and the age-related changes in these features. Some of these features are likely to capitalize on human pattern processing predispositions (i.e., innate or readily acquired) and others on experience. It may be relevant that all of the melodic processing tasks in which infants applied an interval-processing strategy involved the musical interval of a perfect fifth (seven semitones) or the simple integer ratio of 3:2 (Trehub & Trainor, in press). This frequency ratio is present in complex sounds in the natural environment, including speech sounds. If *good form* in general is critical to enhanced processing, diatonic structure being one of many possible instantiations of *good form*, then infants should show comparable enhanced processing for prototypical melodies from foreign musical cultures. Presumably, musical cultures the world over should favor patterns that are congenial to natural perceptual abilities, preferences, and perceptual learning. If exposure, however limited and unsystematic, is critical, then infants from our culture should perform more poorly on *good* foreign melodies than on *good* Western melodies, as is the case for adults (Castellano, Bharucha, & Krumhansl, 1984). There is some precedent for experiential effects in early life, as seen in enhanced processing for mother's over stranger's voice in the neonatal period (DeCasper & Fifer, 1980) and for native over foreign speech sound categories by 10 months of age (Best, Mc-

Roberts, & Sithole, 1988; Werker & Lalonde, 1988; Werker & Tees, 1984). On the other hand, it is probably no accident that the speech sounds of different languages have considerable overlap, their selection being influenced by relative discriminability or ease of processing (Comrie, 1981).

POSSIBLE SIGNIFICANCE OF RELATIONAL PITCH PROCESSING IN INFANCY

What possible functions are served by these relational pitch processing strategies in early life? One such function may be related to the fact that human caregivers reserve a unique vocal register for interactions with their young, a register known variously as *babytalk, motherese*, or *infant-directed speech* (for reviews see Ferguson, 1964; Fernald, 1984; Papoušek, Papoušek, & Bornstein, 1985). The acoustic properties of this register seem to be finely tuned to infants' pattern processing skills and dispositions (Trehub, 1990; Trehub & Trainor, 1990), in the sense that they exhibit a number of music-like features (Fernald, in press; Papoušek & Papoušek, 1981).

Although infant-directed speech differs from adult-directed speech in its higher fundamental frequency (i.e., pitch), increased pitch range, slower tempo, reduced utterance length, and simpler pitch contours (Fernald & Simon, 1984; Papoušek & Papoušek, 1981; Stern, Spieker, Barnett, & MacKain, 1983), it is the pitch contours that are most prominent and distinctive. These contours are relatively few in number, each being used repeatedly with variable content (Stern, Spieker, & MacKain, 1982). Moreover, specific contours (rising, falling, bell-shaped) are associated with distinctive caretaking contexts (Ferrier, 1985; Papoušek et al., 1985; Stern et al., 1982) so that pitch contour emerges as the essence of caregiver communications (Fernald, 1989, in press; Trehub, 1990).

Infant-directed speech seems to be highly effective in modulating attention, arousal, and affect in preverbal infants. When given a choice of infant-directed or adult-directed speech, 4-month-olds attend selectively to the former (Fernald, 1985; Werker & McLeod, 1989), with the pitch patterning or contour being primarily responsible for this preference (Fernald & Kuhl, 1987). It is also the case that exposure to infant-directed utterances of approval heightens positive affect compared to adult-directed utterances (Werker & McLeod, 1989) or to infant-directed utterances of disapproval, even when the language is unfamiliar to infants (Fernald, in press).

There are interindividual and intercultural differences in specific parameters of infant-directed speech such as the absolute pitch level and pitch range (Fernald et al., 1989). These differences reflect,

among other things, the caregiver's vocal tract size (and corresponding fundamental frequency differences), variations in cultural display rules, which encourage or inhibit vocal expressiveness (Fernald et al., 1989), and the caregiver's emotional state (Bettes, 1988; Stern et al., 1982). Nevertheless, the apparent universality of caregiving pitch contours (Fernald et al., 1989; Grieser & Kuhl, 1988; Papoušek & Papoušek, in press) together with their clear efficacy (Fernald, 1985; Werker & McLeod, 1989) suggests a biological basis for the production of such signals, on the one hand, and for infant melodic receptivity, on the other. Later in infancy, pitch contour processing may facilitate the process of language acquisition by directing attention to word, phrase, and clause boundaries (Kemler Nelson, Hirsh-Pasek, Jusczyk, & Wright Cassidy, 1989; Morgan, Meier, & Newport, 1987).

Although a unique vocal register for caregiving is generally viewed as an exclusively human adaptation, some research with nonhuman primates suggests that this might not be the case (Baldwin, 1969; Biben, Symmes, & Bernhards, 1989; Dumond, 1968). Biben et al. (1989) have described a class of squirrel monkey calls that is exclusively infant-directed. In contrast to other (adult-directed) calls, these caregiver signals are characterized by distinctive fundamental frequency (lower), rich harmonic structure, clear tonal quality, and rapid modulations of frequency and amplitude. Moreover, Biben et al. have identified three types of calls in distinct caregiving contexts: (1) maternal calls during dorsal contact or nursing, (2) inspection calls by aunts (female nonmothers) during dorsal contact or nursing, and (3) retrieval. The finding of unique infant-directed vocalizations in squirrel monkeys suggests the possibility of their presence in other nonhuman species. Further progress in elucidating the motivational basis of caregiver signals in nonhuman species may help clarify the biological basis and functional significance of music-like caregiving signals for human infants.

Whereas contour-processing strategies in human infants are of obvious relevance to the reception of infant-directed speech, the function of interval-processing strategies is much less clear. Just as interval processing may be limited to *good* or well-structured melodies in the case of infants (Cohen et al, 1987; Trehub et al., 1990) and to *familiar* or highly overlearned melodies in the case of adults (Attneave & Olson, 1971), so this strategy may be reserved for infants' identification of individual speakers such as their primary caretaker.

Although there is evidence that very young infants can recognize their mother's voice (DeCasper & Fifer, 1980; Mehler, Bertoncini, Barrière, & Jassik-Gerschenfeld, 1978), the basis for such recognition is unknown. Perhaps it is relevant that studies reporting maternal voice recognition have presented extended speech sequences as opposed to single sounds so that the extraction of pitch contours and

interval patterns (i.e., specific melodies) would have been possible. Nevertheless, descriptions of the pitch patterning of maternal speech have focused largely on pitch level, pitch range, and contour, with no identification of interval patterns or actual tunes. It is possible, then, that caregivers have distinctive interval patterns or tunes over and above their species-typical contours so that infants could learn to recognize their mother's unique vocal signature or tunes, just as they quickly learn to recognize her unique olfactory signature or smells (Cernoch & Porter, 1985; Macfarlane, 1975). In a variety of species, infants readily learn to differentiate salient stimuli that are associated with maternal care (Alberts, 1981). Perhaps human infants' precocious perception of contour and intervals will ultimately be linked to their role in fostering optimal emotional states and reciprocal attachment in caregiver and infant. Could there be parallels between human infants' perception of pitch contour and songbirds' recognition of conspecific neighbors and between human infants' perception of intervals and songbirds' recognition of individuals?

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TIMING BEHAVIOR AND DEVELOPMENT: COMMENTS ON SOME ANIMAL AND HUMAN DATA

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ABSTRACT: This paper discusses timing behavior as measured by Fixed Interval (FI), Differential Reinforcement of Low rate (DRL) or Differential Reinforcement of Response Duration (DRRD) performances, in humans and animals at different developmental stages. Infants and rats display similar behavior patterns in FI and DRL. From childhood on, humans develop species-specific behavior patterns in FI, which differ from those of animal species. However, DRL patterns do follow similar developmental trends in animals and humans. These discrepancies and similarities may be explained by the availability of cognitive and linguistic tools in humans, and the degree of schedule constraint on behavior. Motivation and reinforcer variables as well as indices favorable to a cross-specific timing mechanism (such as scalar timing) are briefly commented upon. Available data tend to show that humans shift from contingency-shaped or "animal-like" behavior, in infancy, to rule-governed behavior. This transition is progressive and does not seem to erase forms of adaptation to temporal constraints that humans share with other species.

RÉSUMÉ: Ce texte discute, dans une perspective développementale, la régulation temporelle du comportement obtenue dans les programmes operants à Intervalle Fixe (FI), de Débit de Réponse Lent (DRL) et de Renforcement Différentiel de Durée de Réponse (DRRD) chez l'animal et l'humain. Les très jeunes enfants et les rats produisent des patrons de réponse similaires dans les programmes FI et DRL. Dès l'âge de 5 à 6 ans, les humains développent, dans le programme FI, des patrons de réponse qui diffèrent de ceux des autres espèces. Toutefois, les patrons de réponse enregistrés dans le programme DRL chez l'humain suivent, au cours du développement, des tendances similaires à celles des autres espèces. Ces différences et similitudes peuvent être partiellement expliquées par la disponibilité, chez l'humain, d'outils cognitifs et verbaux, et par le degré de contrainte spécifique à chaque programme de renforcement. Les variables motivationnelles, celles liées au processus de renforcement et les indices favorables à l'existence d'un mécanisme d' "horloge interne" commun à toutes les espèces sont brièvement commentés. Les données disponibles tendent à montrer que, de la très jeune enfance à lâge adulte, l'humain passe d'un comportement "similaire" à celui de l'animal et contrôlé par le seul processus de renforcement à un comportement gouverné par des règles. Cette transition est progressive et ne semble pas éradiquer les formes d'adaptation que les humains partagent avec les autres espèces animales.

Time estimation in animal species has been extensively investigated over the last decades, due to the technical facilities provided by

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operant procedures in the laboratory. Interest has been further stimulated by the discovery that behavior emitted by various species can be described in terms of empirical laws such as the power law and Weber's law (Catania, 1970; Platt, 1979) and by the development of the scalar timing model (Gibbon, 1977). This theory offers a plausible account of various sets of time regulated behaviors in terms of their underlying mechanisms. Historically, the human psychology of time was studied with procedures different from those used with other animals. These procedures, designed for the study of absolute and differential thresholds of duration in humans, collected data based on the subject's verbalizations. The method used for threshold duration could not be used with animals before the operant methodology was developed. Since then, animal psychophysics has been widely studied. The sensitivity of organisms to the duration of external stimuli is only one aspect of the psychology of time. Another is the measure of response timing, i.e., the patterning of overt behavior in relationship to various temporal constraints, made possible as a result of Skinner's (1938) pioneering work. The application of operant procedures across nonhumans and humans over the last 20 years or so has yielded systematic comparisons. Comparing nonhumans and humans is not only of interest because of methodology, but because it addresses the fundamental question of similarities versus differences, of continuity versus discontinuity between animal and human timing behavior, in relationship to the possible role of symbolic processes and language in accounting for discontinuity, if the discontinuity is found.

Data obtained with classical temporal regulation (Fixed Interval, FI) and temporal differentiation procedures (Differential-Reinforcement of Low rates, DRL, and Differential Reinforcement of Response Duration, DRRD) will be successively described and commented upon. For each of these procedure types, two questions will be addressed:

   a) Do adult animals and humans exhibit similarities in response timing?
   b) Do timing performances undergo developmental changes?

A third question will be discussed separately: Do animals and humans share common timing mechanisms?

TEMPORAL REGULATION: THE FI PROCEDURE

The Fixed Interval schedule reinforces the first response emitted after a specified interval of time has elapsed since the last reinforcement. Responses emitted during the interval are without consequences. They are just superfluous. Trained animals such as pigeons

and rats typically develop a particular response pattern: a pause (after each reinforcement) followed by a progressive acceleration of responding, up to the next reinforcement. In a variant of this pattern, animals may, instead of progressively accelerating response rates, maintain a constant rate until reinforcement. This response pattern is labeled "break and run." It has been described mostly with pigeons (Schneider, 1969) but can be observed in other species such as, rats or mice, as well. (For a discussion of response patterning in FI, see Dews, 1978). FI behavior is sensitive to schedule parameters. Pause duration increases and response rates decrease when the interval value increases. It must be noticed here that temporal regulation of behavior (i.e., the pause-response pattern) is not required by the FI schedule. It develops spontaneously as a consequence of training, at least in the "classical" laboratory species such as pigeons and rats. The quality of temporal regulation can be assessed from the cumulative record of responses, the distribution of responses in successive segments of the interval, the duration of the post reinforcement pause or the Curvature Index of Fry, Kelleher, and Cook (1960), that integrates most of the features of performance (Richelle & Lejeune, 1980).

a) Adult Animals and Humans

Whereas adult animals perform as just described, i.e., pause after each reinforcer, and resume responding towards the last part of the interval, adult humans do not. They exhibit either a high-rate (high constant response rates throughout the interval) or a low-rate pattern (one or very few responses at the very end of the interval as can be seen in Lowe, 1979, Fig. 5.1). The high rate pattern is insensitive to schedule parameters. It does not change when the duration of the interval is increased or decreased. In the low rate pattern, response rates depend upon FI value since only one or a few responses are emitted at the end of the interval. As reviewed by Lowe (1979), response patterns may, however, be sensitive to response cost if responding is made more effortful. When response force is increased to a few hundred grams, the high-rate pattern may drift to the low-rate type (Azrin, 1958).

Patterns in humans can also be influenced by conditioning history. Weiner (1965) obtained a high rate FI pattern after a Fixed Ratio (FR) schedule in which reinforcement rate depends upon response velocity. Similarly, previous training with the Differential Reinforcement of Low rate schedule (DRL) which reinforces inter-response times exceeding a critical value, induces a low-rate pattern in FI. Finally, FI performance is highly sensitive to verbal instructions and self instructions. Lippman and Meyer (1967) obtained high rates, low rates or both patterns in different groups after ratio, low rate or mini-

mal instructions, respectively. Humans who receive minimal instructions describe the contingencies as requiring low or high rates when invited to report verbally after the session. They replace the absence of task-specific instructions with their own hypotheses about the contingencies at play and follow self-made rules. Thus, FI performance in human adults seems to obey "high rate" or "low rate" rules, that generate patterns different from those obtained with animals. To sum up, human performance seems to be "rule governed" rather than "contingency-shaped," as is the case in animal species.

Does this mean that animal-like patterns of timing behavior cannot be obtained in human subjects? Matthews, Shimhoff, Catania, and Sagvolden (1977) contend that discrepancies between animal and human FI behavior might be due to procedural differences. If animal-like patterns are to be expected from humans, these should be given minimal instructions, be exposed to response shaping and be rewarded with reinforcers that require a "consummatory" behavior truly interrupting the flow of free operant responding, as is the case with animals. These guidelines, however, led to mixed results, with a high intra- and inter-subject variability in performance. Following an animal-fair procedure with humans does not yield animal-like performances in every case. It is not a sufficient condition to obtain such a behavior.

Other attempts have been more fruitful. Animal-like FI performance can be obtained in adult humans if an observing contingency is added to the operant response. Lowe (1979) instructed humans to push on a response panel to get points that could be exchanged for money at the end of the session. Each response briefly lit the display of a digital clock giving in minutes and seconds the time elapsed since the last reinforcer delivery. A pause-scallop pattern could be obtained with this procedure. Furthermore, performance was sensitive to schedule parameters. Pauses increased and response rates decreased when the interval value increased, as in rats and pigeons. Post-reinforcement pauses plotted against interval duration could be described by power functions $Y = kX^n$ (where Y is the duration of the pause and X the duration of the interval, k and n empirical constants), be it in rats, pigeons or humans, with k ranging from 1.2 to 1.8 and n from 0.63 to 0.81. Thus, providing a response-dependent clock induces an interval-based formulation of the contingencies, obviates the need for covert timing behavior and yields an animal-like FI pattern, sensitive to schedule parameters. In other words, the response-dependent digital clock may have suppressed interference from self-produced conscious interpretations.

If such cues interfere with performances, it might be advisable to study FI behavior in experimental settings where the subject is "unaware" of the contingency at play or in infancy, i.e., at an age where

producing or using cues is highly improbable. Both attempts proved successful.

Bailey and Lowe (1988) instructed adult humans to manipulate a computer keyboard for points which were displayed on the computer screen. The real contingency was hidden. Points were not given for keyboard manipulation, but movements of the swivel chair on which the subjects sat were reinforced according to a FI schedule. Keyboard response patterns were disorderly whereas chair movements followed the typical pause-response pattern. Furthermore, the subjects could not describe the contingencies at play when questioned after the session. The confirmation of such data would show that "awareness" about the contingencies, which generates self-produced cues or rules, can mask or interfere with schedule control.

The issue of learning without "awareness" (which does not mean without "consciousness") has been extensively studied some 30 years ago. It has several aspects that cannot be discussed here (see among others, Nisbett & Wilson, 1977; Schacter, 1987; Wearden, 1988). Participants may be "unaware" of the response (small movements as in Hefferline, Keenan, & Harford, 1959; autonomic response such as in Brener, 1977), or of stimuli ("subception," as in Lazarus & McCleary, 1951, where a galvanic skin response can be elicited by unnoticed stimuli). They also may report efficient response strategies (i.e., strategies yielding reinforcers) which do not match with the contingencies and thus are incorrect from the experimenter's point of view, as is, for example, the case when humans on DRL report complex sequences of behavior ending in the operant response (Wearden, 1988, labels these reports "coincidental awareness"), or when they make erroneous reports about their own behavior or experimental events. These studies are plagued with methodological problems and often lack appropriate means to detect participant's "awareness" (Eriksen, 1960). However, procedures such as the one reported above, in which the response-reinforcer contingency is hidden behind false information and instructions might prove an efficient strategy to disentangle the variables at work.

Lowe, Beasty, and Bentall (1983) reported FI performances of two infants aged 9 and 10 months. The infants sat in a high chair or on their mother's lap, in front of a big horizontal cylinder that could be touched (response). They were reinforced with music or food items. After response shaping by successive approximations, infants were submitted to FI schedule values ranging from 10 to 50 s. Sessions usually ended after 12 to 30 reinforcers had been obtained. Performance in both infants closely resembled the scalloped pattern of animals. The second criterion, i.e., the sensitivity to schedule parameters, was also met. The post-reinforcement pause was a negatively accelerated increasing function of schedule value, as can be seen on
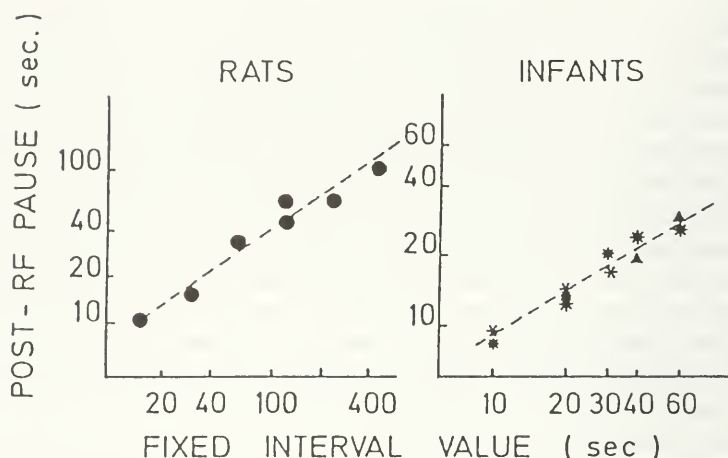
FIGURE 1. Duration of the post-reinforcement pause (ordinate) plotted as a function of FI value (abscissa), in rats (left) and human infants (right). Redrawn and modified after Figure 9 (p. 177) from Bentall et al. (1985). Abscissa and ordinate are in log scale.

the right part of Figure 1; furthermore, response rates were inversely related to the duration of the interval, as in the case with rats (Bentall, Lowe, & Beasty, 1985).

Scarce as they are, experimental results reported above show that animal-like FI behavior can be obtained in humans 1) if they are distracted from self-produced cues or rules by an external clock or if they are "unaware" of the contingency and 2) if they are conditioned at infancy, i.e., before mastery of language and crucial language-related cognitive tools.

b) Developmental Changes

The importance of verbal factors, as emphasized by Lowe (1979), has been confirmed by subsequent developmental research (Pouthas, 1985; Bentall & Lowe, 1987; Bentall et al., 1985). Whereas infants follow a pause-scallop pattern in FI, the behavior of children aged 2½ to 4 years is highly variable and irregular. It is accompanied by unsystematic and diverse verbalizations, which probably interfere with performance. Children cannot refrain from responding and are unable to follow low-rate instructions over the complete training period. Control by instructions is more readily achieved in children aged 5 to 9 years. The inability to comply with a low-rate instruction in the youngest subjects is congruent with Luria's (1961) analysis, according to which the use of verbal skills for regulation of motor behavior and
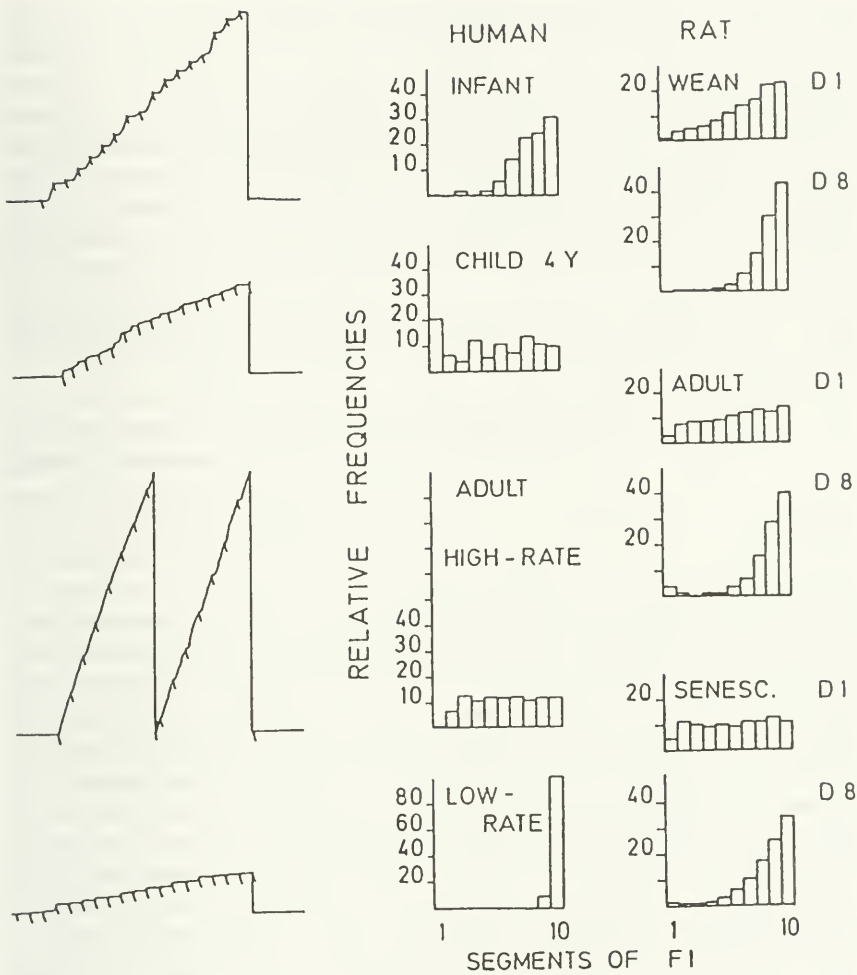
FIGURE 2. Performance of humans (left and middle columns) and rats (right column) on a FI 60 s schedule (unpublished data). Humans: the left column shows sample cumulative records of responses; the middle column presents the same behavior as relative frequency distributions of responses per successive segments of the interval. Rats: the right column presents relative frequency distributions of responses per segments of the interval. In each column, and from top to bottom: performance at different ages (weaning, adulthood and senescence for rats; infancy, childhood and adulthood for humans). For rats at each age: average performance at training Days 1 (D1) and 8 (D8).

self-control is not functional before the third or fourth year of life. From about 5 years on, the irregular FI response pattern evolves progressively towards the adult-like low- or high-rate patterns. Coherent descriptions of the contingencies and related response rules appear simultaneously. The evolution of FI performance, as illustrated in the left part of Figure 2, thus seems to mirror the development of language, i.e., the development of the ability to describe accurately the own behavior and to formulate response rules that will be translated accurately at the behavioral level. Cumulative records of performance match with verbal comments or rules only in humans above 5 to 6 years, i.e., at an age where response patterns resemble those of adults (two cumulative records at the bottom left of Figure 2).

In a related developmental study (Lejeune, Jasselette, Nagy, & Perée, 1986), weanling (20-day-old), adult (3-month-old) and senescent rats (24-month-old) were subjected for 8 days to a massed learning procedure. They performed five 30-min FI 60 s sessions a day. Data showed that the rate of FI acquisition is inversely related to the age of the subjects. Weanling rats obtained the highest performance scores in FI, followed by adult and senescent rats, as can be seen on the right part of Figure 2. At the first day of training, the temporal patterning of responses was inversely related to the age of the subjects: weanling rats displayed a clearcut increase in response rate over the successive segments of the interval (right part of Figure 2). Response rates also were inversely related to the age of the subjects. This developmental trend does not seem to reflect a fundamental difference in the underlying timing mechanisms. It is however worth noticing that the highest response rates were correlated with the longest post-reinforcement pauses and the highest Curvature Index values in the weanling rats, and that these features remained significantly different from those exhibited by adult and senescent subjects, over the first 20 to 30 sessions. The high response rates in weanling rats may be related to age-specific high levels of general activity (Moorcroft, 1971). However, operant activity is not spread out over the complete fixed interval. Responses are efficiently inhibited after the delivery of each reinforcer. Weanling rats displayed various types of collateral activities during the post-reinforcement pauses. Three major types emerged after 12 to 15 sessions: ano-genital grooming, tail-nibbling and "sleeping" in a curled-up position (head bent under the body and closed eyes). Various collateral activities were also noticed at the other ages, but to a lesser extent. We have so far described similarities as well as differences between developmental data of animals and humans in FI. Before further discussing these data, some results obtained with temporal differentiation procedures will be presented hereafter.

TEMPORAL DIFFERENTIATION: THE DRL AND DRRD PROCEDURES

In the Differential Reinforcement of Low rate (DRL) schedule, reinforcement is contingent upon response spacing. The DRRD schedule, a variant of DRL schedule, reinforces response durations instead of Inter-Response-Times (IRT). These schedules are labeled "temporal differentiation" schedules because they reinforce and select a temporal characteristic of the operant: its delay with regard to the preceding response or its duration. They are fundamentally different from FI. Reinforcement is contingent on the temporal regulation of behavior, whereas it is not in FI. To assess the quality of performance, IRTs or response durations can be sorted according to their duration and cast in time bins. Trained rats exhibit a clearcut modal IRT or response duration, close to the reinforcement criterion.

a) Adult Animals and Humans

As was the case with FI, recent data have addressed both the comparative and developmental aspects of response timing in animals and humans. Data obtained with adult animals in DRL or DRRD depend on multiple factors among which are the length of the critical IRT or response duration, the species and the nature of the operant response. One data sample will be described here. It is representative of the performance obtained in pigeons with a perching response.

Adult homing pigeons were trained to hop on a perch protruding from the rear wall of their conditioning cubicle and to step quickly off. After acquisition of the brief perching response, the experimenter reinforced inter-response-times between successive brief perching responses. Baseline data were collected for DRL values of 10, 20, 30, 40, 50, 60, and 70 s. IRTs were cast in bins and Gaussean functions could be fit to the relative frequency distributions of temporal estimates for each schedule value (Jasselette, Lejeune, & Wearden, 1990). Peaks were localized on the Gaussean curves and coefficients of variation were computed (i.e., the ratio between the standard deviation and the peak of the distribution of temporal estimates). Performances displayed two major features, as can be seen on the left part of Figure 3. First, peak time matched with, or was close to the critical IRT at each schedule value. Secondly, the coefficient of variation remained roughly constant, up to DRL 50 s. It tended to increase at DRL 60 and 70 s, which might indicate a slight loss in the accuracy of behavior. Overall, the values of the coefficient of variation remained between .20 and .30, a range obtained in other parametric experiments with DRL or reinforcement of response latency schedules (Catania, 1970;
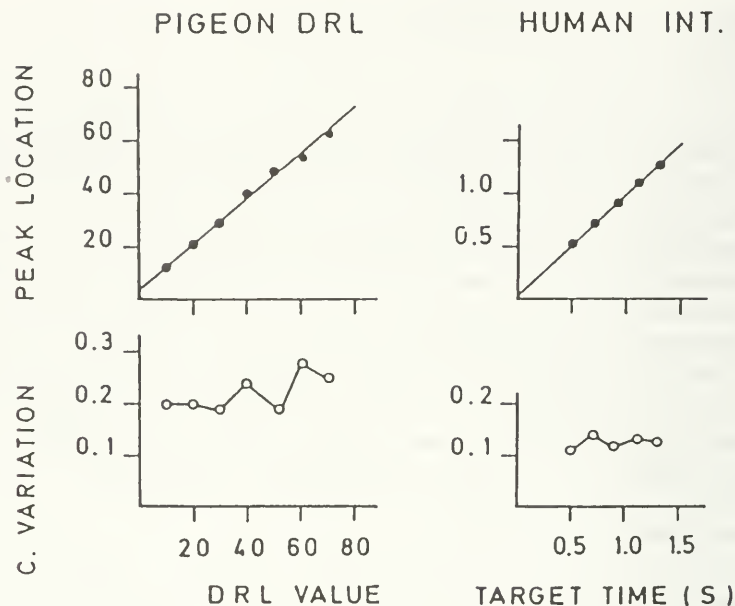
FIGURE 3. Top: location of peaks of Gaussean functions fitted to relative frequency distributions of temporal estimates. Left: IRT data from pigeons at DRL 10, 20, 30, 40, 50, 60, and 70 s with a perching response. Right: interval production data from humans (target times: .5, .7, .9, 1.1, and 1.3 s; data from Wearden & McShane, 1988). Regression of peak times against target times yield slope, intercept and r^2 (proportion of variance accounted for) values of .87, 3.71, and .99 for pigeons, .96, .05, and .99 for humans. Bottom: coefficients of variation (c. variation, i.e., the ratio between standard deviation and peak of the distribution of temporal estimates) for pigeons (left) and humans (right).

Platt, 1979). The mean temporal estimate and the coefficient of variation may be considered as reflecting the subject's representation of the schedule parameter and the subject's sensitivity to time (Roberts, 1981).

Bearing the language issue in mind, experiments with adult humans were designed to control the verbal factor. This was achieved either by choosing schedule parameters which render conscious time-spanning or counting strategies difficult (Wearden & McShane, 1988) or by requesting a deliberate chronometric counting (Wearden, 1991a).

In the first experiment, Wearden and McShane instructed people to produce empty time intervals of .5, .7, .9, 1.1, and 1.3 s. The participants held one button in each hand and had to press them in succession to start and stop a milliseconds counter. Accurate feedback to

two decimal places in seconds was given after each response. Dura-
tions to be produced were scheduled in a random order. Data analysis
as described above for the pigeon DRL experiment yielded accurate
mean interval productions as well as constant coefficients of variation
within a .10-.15 range (right part of Figure 3), which is much lower
than values obtained with the pigeons.

In the second experiment, intervals to be produced were 2, 4, 8,
16, and 32 s and the humans were requested to count (Wearden,
1991a). Means and coefficients of variation of the distribution of tem-
poral estimates were obtained from 14 people. As in the preceding
experiment, mean intervals matched target time. However, coeffi-
cients of variation declined sharply (from .09 to about .05) between
target times of 2 and 8 s, without further change at 16 and 32 s.
Striking features of these results, with regard to the preceding ones,
are the progressive decline of the coefficient of variation and its very
low absolute value.

In a research by Laties and Weiss (1963), human adults were
requested to space leverpresses by at least 24 s. Each correct IRT lit a
lamp and incremented a counter. Correct responses were rewarded
with money at the end of the session. The modes of the IRT distribu-
tions of 11 out of 14 participants were between 24 and 28 s (they
overmatched target time) and the spread of the IRT distributions was
very narrow (as can be seen for example on the bottom left graph of
their Figure 2).

In an experiment where the authors served as subjects, Zeiler,
Scott, and Hoyert (1987) described interval productions of .5, 2, 8, and
32 s. In one of their conditions, those intervals had to be produced
without an upper boundary. A "correct" feedback light flashed after
intervals equal to or greater than the minimum target time. An "er-
ror" light followed responses that were too short. After completion
of the experiment, the authors reported that they had been unaware
of counting or performing other time-spanning collateral behavior.
Mean times produced increased with the minimum target duration.
They also overmatched the minimum target duration, as in Laties
and Weiss (1963). The coefficients of variation, although following
different trends in individuals (increase, decrease or stability) were in
the .10-.15 range found by Wearden and McShane (1988) with their
short-duration interval production task (.5 to 1.3 s).

It follows from these experiments that 1) interval production in
adult humans might be similar to animal performances (i.e., accurate
mean and constant coefficient of variation) if chronometric counting
is rendered inoperant; 2) human performances might differ depending
on whether chronometric counting is or is not involved (Wearden,
1991a); 3) differential response feedback seems to play a secondary
role and, 4) humans are more sensitive to the temporal criterion than

pigeons and rats. Their temporal estimates are within a narrow range around mean values. Such a species-related difference has already been described in psychophysics of time where Weber fractions of humans undermatch those found in animal species.

b) Developmental Changes

Given that human adults emit temporal estimates with an accurate mean value and a constant coefficient of variation when they are prevented from counting or do not use conscious time mediating strategies, temporal regulation was, as in FI, explored at an age where such tools are probably not at hand. Developmental data are available for two infants and young children (see left part of Figure 4). Responses are usually a button or leverpress. Reinforcers are a small piece of food, a slide or puppet display. Infants and young children are able to reduce response rate over successive sessions (Pouthas, 1985; Weisberg & Tragackis, 1967). Pouthas and Jacquet (1983) further showed that 18- to 24-month-old children trained on DRL 5 s can fill interresponse times with collateral activities such as systematic locomotion or furniture manipulation. Between 1 and 3 years, they can inhibit motor behavior for a while but are unable to precisely time their operant responses. As infants do, they emit very high proportions of too short IRTs as well as numerous long ones, far exceeding the minimum critical delay. As a consequence, their IRT distributions are in some cases "U" rather than bell shaped. More precise temporal differentiation seems to develop around the age of 7 years, as the capacity to inhibit motor activities matures (Stein & Landis, 1978; Macar, 1988). Five-year-old children move a lot during experimental sessions. Seven-year-olds remain quiet and count (Pouthas & Jacquet, 1987). As was the case in FI, 4½-year-old children can benefit from instructions to wait between successive responses and from descriptions of the temporal characteristics of the task. They also are able to self-instruct ("I must wait"). However, most of the youngest cannot explain the "rule of the game," even if their behavior is adjusted to the contingencies.

Concerning the relationship between operant behavior and language, two opposite theoretical positions can be distinguished (see Wearden, 1988; Pouthas, Droit, Jacquet, & Wearden, 1990). The first, labeled "verbal control" or "cognitive," considers that cognitive or verbal changes should precede changes in nonverbal behavior. According to the second, labeled "epiphenomenalist," nonverbal behavior is directly controlled by the reinforcement contingencies, verbalizations being a posteriori by-products derived from the observation of relationships between nonverbal behavior and its consequences. Verbal behavior would thus not be the prior and necessary condi-
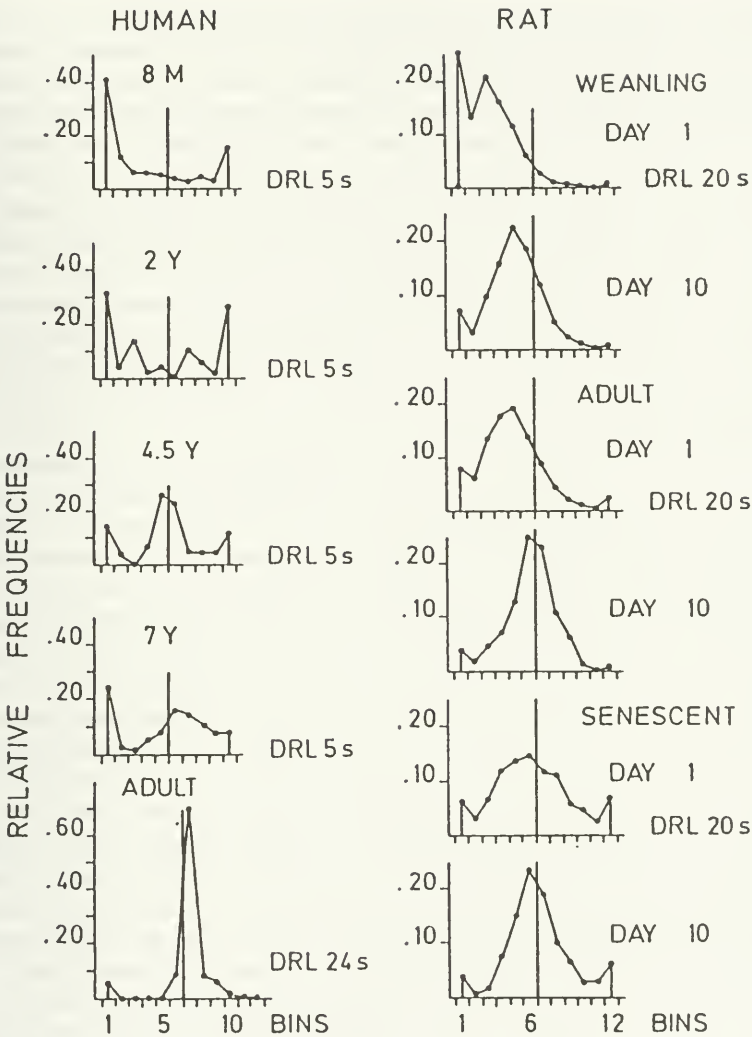
FIGURE 4. Sample relative frequency polygons showing the distribution of temporal estimates (IRTs) in 10 or 12 bins for humans (left column) and rats (right column). From top to bottom: IRT distributions at different ages in humans (M = month, Y = year) and rats (at each age, average performance at training Days 1 and 10). The IRTs at the right of the vertical lines are reinforced. Notice the different ordinate scales for humans and rats. Bottom left graph: redrawn and modified after Laties and Weiss, 1963, Figure 1 (p. 87); other human data: redrawn and modified after Pouthas, 1985, Figures 3 (p. 106) and 4 (p. 107).

tion for changes in nonverbal behavior to occur. Opposing a cognitive and epiphenomenalist theory is probably a crude oversimplification. A third view, possibly closer to empirical and developmental descriptions could be phrased as follows: nonverbal contingencies would suffice to account for a number of aspects of timing behavior (especially those referred to as "animal-like"), especially in infants and human adults under certain conditions; cognitive and verbal skills would enter the picture at a certain stage of development, initially as a simple, more or less accurate description of behavior and contingencies; and these higher order skills would eventually take over control of nonverbal behavior, after the current concept of top-down causation, or after the classical view of Luria (1961) as to the regulatory role of language on motor action, or the "rule-governed" behavior concept as proposed by Skinner (1974).

The role of language in temporal differentiation performance has been recently investigated in children aged 4½, 7, and 11 years, submitted to the differentiation of a button press duration, i.e., a DRRD schedule (Pouthas et al., 1990). Each response was followed by a question about the schedule requirement (verbal probe). Other groups of children were interviewed after the experimental session. Results showed that overall performance scores were higher and increased with age in the probe groups only. A clearcut relationship between verbalizations related to time and accuracy of response durations emerged only in the 11-year-old probe group. For these children, time-related verbalizations were translated into behavior: relationships between temporal verbalization and accurate performance seemed to be causal rather than correlational. Most of the younger children displayed no correlation between verbalizations and performance accuracy. However, accurate response timing was possible without verbalizations related to the temporal aspects of the task. Children aged four-and-a-half to six years often expressed simple response rules ("I must press the button") followed by an accurately timed response. Further, they rarely formulated time-related rules when questioned. However, as noticed by Pouthas (1989), absence of correlations between behavior and content of overt verbalizations does not disprove rule-governance. Congruent verbal behavior is not a prior or necessary condition for accurate changes in nonverbal behavior to occur. In other respects, the question as to whether young children have a time concept based on a perceptual experience of duration rather than one derived inferentially from non-temporal cues, such as speed, distance, succession (Piaget, 1969) is still open to inquiry (Richie & Bickhard, 1988).

Taken together, these developmental data again tend to show that humans shift from contingency-shaped (in infancy and early childhood) toward rule-governed behavior (from late childhood on) or

from, as Kendler and Kendler (1962) put it within another context (discrimination learning), non-mediational or animal-like learning to learning mediated by language. Early childhood is characterized by a dissociation between saying and doing, between rules and performance. As was the case in FI, performance seems again to mirror the development of language.

Developmental data on temporal differentiation in animal species is available for albino rats (Lejeune & Jasselette, 1987; Lejeune, 1989). Weaning (20-day-old), adult (3- and 7-month-old) and senescent rats (24-month-old) were submitted to a DRL 20 s procedure. They performed 4 sessions a day, for a 10-day period. Each session lasted for half an hour, 250 responses or 40 reinforcers, whichever came first. The accuracy of performance was directly related to the age of the rats, as can be seen on the right part of Figure 4. Senescent rats emitted the highest median IRTs. They also earned the highest number of reinforcers, followed by adult and finally weanlings. Response rates were, as in FI, directly related to the age of the rats. Inter-response-time distributions showed that weaning rats emit high proportions of too-short IRTs, a feature that is almost totally absent in senescent rats. The old rats were most efficient but the spread of the IRT distribution around the modal IRT value was larger than in adults. Age-related differences faded out at the end of the 40 sessions run. An ANOVA computed over the last 12 sessions did not reveal significant differences.

DRL acquisition is age-related in the albino rat, as was FI acquisition. It is noteworthy that, whereas high response rates typical of weaning age could be inhibited in FI (post-reinforcement pauses often exceed 40 or even 50 s), they were not in DRL. This is congruent with the often described FI-DRL paradox. Animals fail at inhibiting responses when this inhibition is requested for reinforcement to be delivered. On the other hand, when this inhibition is not requested, as in FI, it spontaneously develops. Collateral behaviors identical to those observed in FI were found in DRL.

CONCLUSIONS FROM FI AND DRL SCHEDULES

Comparative and developmental data obtained in animals and humans, as reviewed above, suggest that:

1) Acquisition of FI and DRL behavior is age and schedule dependent in animals as well as in humans.

2) Infants or children display patterns of behavior which are somewhat similar to those described for weanling rats.

3) Transition from contingency-shaped to rule-governed behavior in humans is progressive and parallel to the development of cognition

and language. However, although adult humans display rule-governed behavior in DRL and FI, rules match with contingency requirements only in DRL whereas they do not in FI. Rule-governed DRL behavior in humans is much more "animal-like" than is rule-governed FI behavior. The reasons for this discrepancy have long been identified (Lowe, 1979). Fixed Interval per se sets no constraint on response output. The rate of reinforcement does not depend upon the rate or patterning of responses within the interval. As a consequence, several response patterns may be reinforced. In DRL, on the other hand, response rate is directly tied to rate of reinforcement. This constraint is powerful enough to select and mould cognitive strategies that fit with the contingency. Humans become aware of the critical delay (or response duration in the case of DRRD) and most often resort to overt or covert counting-like routines. The only difference between a child aged 6-7 years and an adult will thus be the degree of mastery of chronometric units as well as the capacity to focus attention and inhibit motor output. FI and DRL behavior in adult humans are both rule-governed but the nature of the rule depends on a "degree of behavioral freedom" that is large in FI, narrow in DRL. This does not explain why FI patterns in adults resort to clearcut high- or low-rate types. It only explains why multiple patterns might occur. A similar distinction was made by Wearden (1988), in terms of informationally rich (DRL) or poor schedules (such as FI), and by Galizio (1979) in terms of contact or no-contact schedules where "incorrect" behavior induced by false instructions can be reinforced and thus never matches with the "schedule typical" behavior of animals.

4) Transition from contingency-shaped to rule-governed behavior in humans does not eradicate forms of adaptation that humans share with animal species. Animal-like FI behavior was obtained in adult humans with a hidden FI contingency (Bailey & Lowe, 1988) and with an observing contingency added to the operant response (Lowe, 1979). However, the ability to make use of information provided by clocks is not restricted to the human species. Several experiments have shown that the performance of animals, be it in FI or DRL, can be controlled by external stimuli varying as a function of time (for a discussion about temporal regulation and external cues, see Richelle & Lejeune, 1980).

5) Animals and humans display collateral behavior between operant responses in DRL or during the post-reinforcement pause in FI, i.e., overt time-spanning activities such as fur grooming or tail nibbling in rats, nail plucking or drinking in children. These observations extend the generality of collateral behavior from animal to human species. The origin and functions of these collateral behaviors have been discussed elsewhere (Staddon, 1977; Richelle & Lejeune, 1980). There is no doubt that both animals and humans can benefit

from these time-bridging strategies. As shown by Pouthas (1985), very young children in DRL can refrain from responding by relying upon some collateral motor rhythm.

6) Human infants and rats at weaning age are highly sensitive to the FI schedule. This strengthens the analogy between the periodic delivery of the reinforcer in FI and the "Zeitgebers" in chronobiology. Both are events from the surrounding which synchronize behavior. FI performance would be sort of a behavioral link between acquired temporal regulations and biological rhythms. The synchronizing power of the periodic delivery of the reinforcer is further stressed by the fact that young rats and young children emit numerous very short IRTs in DRL and seem unable to efficiently inhibit motor output in this operant contingency.

7) The operant behavior of young children aged 4½ or 7 seems to be mostly contingency-governed. Language seems to gain a causal role only later on, as the data from 11-year-old children submitted to response duration differentiation tended to show. The probing procedure, i.e., questioning children after each trial about the "rule of the game," does not inform about the role of language in the regulation of ongoing behavior. It sheds light on the relationship between response timing and the search or discovery of rules which might influence subsequent nonverbal behavior. However, resorting to a macrovariable such as "language" is void of explanatory value. Refined experiments are needed to isolate the critical factors at play.

DO ANIMALS AND HUMANS SHARE A COMMON TIMING MECHANISM?

The main theoretical account of timing performance in animal species is scalar timing (Gibbon, 1977, 1991; Gibbon, Church, & Meck, 1984). According to this theory, the hypothetical timing system has two major components: an internal clock which reflects the passage of time and a memory of the critical times associated with reinforcement in the past. Under a procedure such as DRL, the animal might start the clock with each response and end an interresponse time as the clock reading becomes close to the remembered reinforced IRT. Behavior based on a scalar process should have two properties. The first is the accuracy of the mean, i.e., average time estimates should match with reinforced time (in a DRL 20 s schedule, the mean IRT should match with the 20 s critical delay). The second is the constancy of the coefficient of variation, over a range of schedule parameters: the standard deviation of the temporal estimates should be a constant fraction of the mean. This property is congruent with the classical form of the Weber law which requires that the Weber fraction remains constant when durations to be estimated vary.

To evidence scalar timing in animal or human performances is not an easy task. Timing is often entangled with nontiming processes, which may distort the behavioral expression of the underlying timing mechanism. For example, DRL behavior is extremely sensitive to fluctuations in the level of motivation of the subjects. Even if, under favorable circumstances, the mean IRT matches with the DRL requirement, it will no longer be the case if the animal is hungry. The central tendency of the IRT distribution will shift to the left and undermatch target time, because increased hunger triggers high response rates which lower the mean IRT. Procedures have been designed, which allow for the isolation of "pure timing," uncontaminated by fluctuations in response rate. The most studied is the "peak procedure" which derives from a discrete trial FI procedure where intervals are signalled by an exteroceptive stimulus. In the peak procedure, some intervals are longer than the basic FI duration and are not reinforced (test intervals). After extensive training, response rate functions in the test intervals have a Gaussean-like shape, on which two crucial features can be isolated: peak rate, i.e., the highest response rate emitted at a given moment in the interval, and peak time, i.e., the precise moment at which peak rate occurs. Peak time is considered as the unbiased estimate of the moment at which reinforcement should occur, because it is not altered by a change in response rate which might be induced by manipulating the probability of the reinforcer (Roberts, 1981). This procedure has so far been tested with pigeons and rats, and over a limited range of critical values (10 to 50 s or so). Peak procedure data support scalar timing theory. Curves fitted to the response rate versus time functions did show that peak time matched with FI value and that the coefficient of variation of the fitted curves remained constant.

An evaluation of the scalar model with more classical procedures such as FI, DRL or duration reproduction has been undertaken, with mixed results. In some instances, and over a limited range of schedule parameters, scalar timing seems to hold. It was the case with the above described DRL perching behavior of pigeons. It seems also to be the case with some sets of FI data (Gibbon, 1977; Wearden, 1985) and with a duration reproduction procedure designed for pigeons (Zeiler & Hoyert, 1989). It also is the case with short interval production in humans (Wearden & McShane, 1988), and with long interval production without conscious chronometric counting (Zeiler et al., 1987, although these authors claim that their data do not fit with scalar timing theory). Some favorable evidence was also found with bisection and temporal generalization procedures which are closer to the psychophysical time estimation procedures used with animals (Allan & Gibbon, 1991; Wearden, 1991a, 1991b).

The claim that scalar timing mechanisms are common to human

and animal species would be premature. Considering data limited to animal species, several problems arise if one tries to reconcile different levels of performance accuracy with a scalar timing mechanism. This has been illustrated with FI data from various animal species: cats, rodents, birds, fish, and a freshwater turtle (Lejeune & Wearden, 1991). These various species were submitted to three to six FI requirements ranging from 30 to 900 s. Fixed interval response rate functions were fitted with Gaussean curves whose peak was forced at FI value. Within a species, coefficients of variation that were derived from the fitted curves were constant over some but not all FI values. They tended to increase with the duration of the interval. Furthermore, species differed markedly in the value of their respective coefficients of variation (the lowest being found in cats, the highest in the freshwater turtle). Even if these data could somehow be reconciled with scalar timing within a two-process model deriving performance from the interaction of a scalar timer and a nontiming process, the possibility of species-specific differences in timing capacity could not be ruled out. The weakness of such a two process model derives from the fact that variations in timing behavior cannot unambiguously be related to changes in one, the other or both interacting processes. The coefficient of variation cannot be taken as reflecting the "pure" functioning of the scalar timing mechanism. In other words, scalar timing theory is difficult to test. The quest for (a) timing mechanism(s) is at present torn between opposite positions. The first favors interspecies generality of a single mechanism (such as scalar timing). The second supports the view according to which several different timing processes might be involved, each tailored to a particular set of temporal contingencies (Macar, 1985). Both positions are at risk, the former of abusive generalization, the latter of generating only ad hoc models.

   Much remains to be done to avoid far-fetched speculations. Differences or similarities that still have to be discovered might further be analyzed within an anagenetic perspective in comparative psychology (Rensch, 1947). This approach focusses on levels or grades in behavioral plasticity or versatility. It is essentially concerned with the range of behavior that animals can reveal when they are faced with challenges which differ meaningfully from those encountered in their natural habitat (Gottlieb, 1984). Suggestions made by Bitterman (1960, 1965) or Gottlieb (1984) among others, clearly indicate methodological guidelines which might be followed: compare closely and remotely related species, submit species to experimental alteration of the species-specific ecology and challenge them with species-atypical tasks. Bitterman (1960) further suggests to control sensorimotor and motivational factors by their systematic variation. A comparative psychology of time within the anagenetic perspective would also request that the species be submitted to an array of tasks or learning

situations which differ in complexity, in order to avoid conclusions based on artifactual differences (Bitterman, 1965). These recommendations, some of them made long before quantitative models of timing were designed, should not be overlooked if a valuable comparative psychology of time is to be developed.

Methodological variables are of prime importance, not only to test the generality of a model of timing, but also in comparative and developmental psychology. Perone, Galizio, and Baron (1988), among others, stress that variables such as the manipulandum or the reinforcer cannot be considered equivalent at different ages. They furthermore contend that crucial causal factors are difficult to isolate, entangled as they are with several other variables of lesser importance.

The methodology issue was pervasive in the analysis presented above. Two independent variables, which are particularly controversial within the human/animal comparison, will be briefly commented upon: the level of motivation and the reinforcer.

Humans do not usually display "considerable enthusiasm" for conditioning tasks, as Church, Getty, and Lerner (1976, p. 309) wrote about rats performing on a duration discrimination paradigm. They, nevertheless, do work for reinforcers with a very low nominal value and even do not consume the food reinforcers dispensed to them, as reported in Wearden (1988). For a rat, accurate responding can be an affair of life or death, but not for humans. Neither are schedule constraints equivalent, nor are the respective motivational states. Wearden (1988) suggests that humans primarily work to get information relevant to the task. Reinforcers also should be considered in terms of their informative rather than hedonic value, as influencing response strategies rather than directly shaping behavior. As Wearden notes, arguing that differences between animal and human performances are due to reinforcement magnitude effects is irrefutable because the operation of equating reinforcement is impossible to specify.

Sensitivity to information or apparent insensitivity to the hedonic value of the reinforcer are, however, not exclusive attributes of the human species. First, information can change animal behavior. Feedback stimuli following responses and dispensing information about their accuracy improve performance, as do stimuli redundant with the reinforcer. Animals also work to get information about the remoteness or probability of reinforcers (Hendry & Dillow, 1966). Secondly, animals such as pigeons can string together thousands of unreinforced responses, as is often the case in DRL schedules with critical delays exceeding 30 s or so. This apparently gratuitous and perseverative pattern of behavior (which results from reinforcement history and also depends upon the nature of the operant) has never been considered as disproving the potency of the hedonic value of the rein-
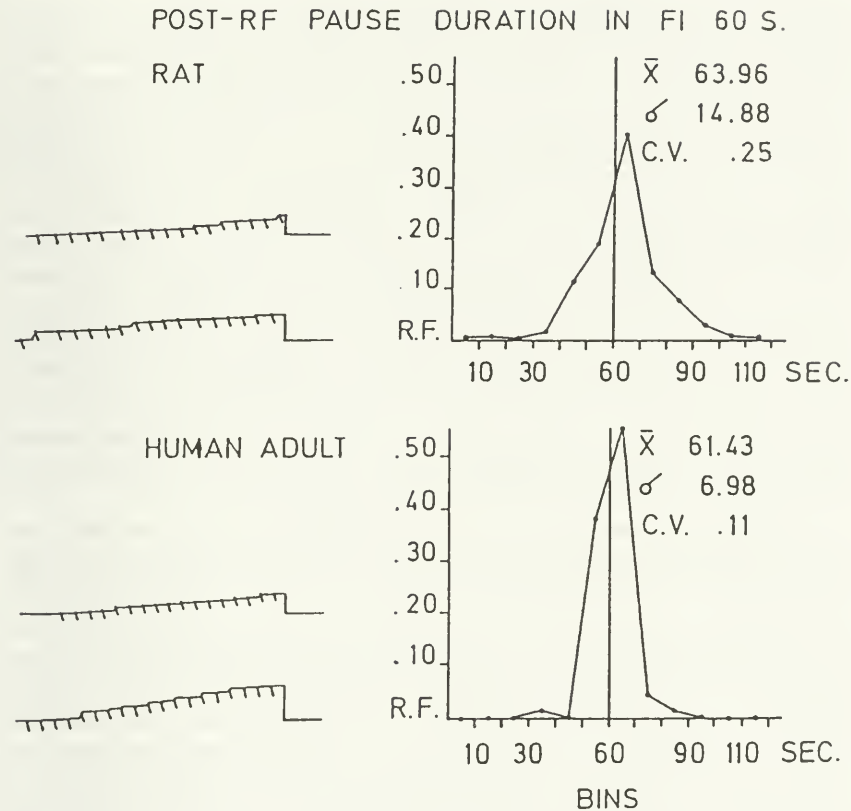
POST-RF PAUSE DURATION IN FI 60 S.

FIGURE 5. Sample cumulative records (left) and distributions of post-reinforcement pause durations in FI (right) for one rat at Day 16 on an around-the-clock schedule (top) and one adult human (bottom). Ordinate of the polygons: relative frequencies (R.F.); abscissa: time bins, with vertical lines at FI value (60 s). The Figure is drawn from unpublished data.

forcer. Human and animal species might differ by the relative balance between hedonic and informational aspects of the reinforcer, hedonic aspects being predominant in animals, informational ones in humans. Whether such subtle differences might lead to a revision of reinforcement theory is a question under debate (Wearden, 1988).

Differences between animal and human performances in temporal regulation or differentiation schedules are not always clearcut. Some differences may just be the consequence of our ignorance about several features of schedule control. For example, FI behavior somehow similar to the low-rate pattern typical of human adults (i.e., one or just a few responses per interval, on the basis of chronometric

counting) can be obtained from adult rats on an around-the-clock Multiple FI/Extinction schedule, where 30-min FI 60 s sessions alternate with 90-min rest periods, the animals thus performing 12 half-an-hour sessions a day (Figure 5). Within the same line, Wanchinsen and Tatham (1989) contended that the ratio- or interval-like behavior patterns typical of adult humans in FI are a mere consequence of their complex experimental history and might not be considered as reflecting features exclusive to the human species. Indeed, Wanchinsen and Tatham obtained human-like FI patterns in rats pre-trained on a Variable Ratio schedule. As Lowe (1979) reported, a high-rate FI pattern may be changed to a low-rate one if the response force is increased from a few to several hundred grams. A similar result might be achieved if humans were trained on high-duration intervals lasting for several minutes. Effortful response requirements would probably suppress superfluous behavior, animals and humans tending towards an optimal cost-benefit trade off.

The data presented above were sampled from a large set of experimental results. However, they do not bear upon all aspects of timing. For example, psychophysics of time has not been discussed (Macar, 1985). The elements gathered so far from comparative and developmental experiments tend to indicate that the most sophisticated timing skills of humans as exhibited when they resort to verbal interpretations and rules, are probably rooted in preverbal or animal-like patterns of behavior. It remains that, endowed as they are with refined verbal and cognitive capacities, humans will conserve primacy on animal species, in terms of rapidity of acquisition, ability to promptly shift behavior and fine-tuning of performance, as sensitivity indices such as the Weber fraction and the coefficient of variation tend to show.

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ERRATUM

Wallace, R. J., & Barnett, S. A. (1990). Avoidance of new objects by the black rat (*Rattus norvegicus*) in relation to object presentation and object change. *International Journal of Comparative Psychology, 3*, 253-265.

The caption for Figure 3 should have read "Each panel presents the mean of the latencies for the U- and C-arms on each trial for four rats. Dashed lines indicate lost data for two rats on trial 14."

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